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THE UNIVERSITY OF ALBERTA

SOME LIMNOLOGICAL FEATURES OF A NORTHERN CANADIAN RIVER, THE KAKISA RIVER, NORTHWEST TERRITORIES, WITH SPECIAL REFERENCE TO THE LIFE CYCLES OF SOME AQUATIC INSECTS

© DONALD R. MUSBACH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1977

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Some Limnological Features of a Northern Canadian River, the Kakisa River, Northwest Territories, with Special Reference to the Life Cycles of Some Aquatic Insects" submitted by Donald R. Musbach in partial fulfilment of the requirements for the degree of Master of Science.

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External Examiner

Date 5 May 1977

ABSTRACT

Some physical and chemical features of the Kakisa River, Northwest Territories, were monitored during 1972 and 1973, and the life cycles of six aquatic insects were studied during this period. Geological, climatological, and general physiographic features of this region are described and an attempt is made to correlate these general features and the specific limnological characteristics of the river with the biological aspects studied. In this way an initial ecological characterization of the river is provided.

Physical features monitored included discharge and related parameters, temperature, turbidity, color and conductance. Chemical features monitored included dissolved oxygen, hardness and alkalinity, and pH; a variety of other chemical constituents were also measured.

Life history information for aquatic insects was obtained primarily by means of dip-net sampling and emergence traps. The life cycle of *Pteronarcys dorsata* (Say) is probably completed in two years, *Isoperla transmarina* (Newman) in one year, *Epherema simulans* Walker probably in two years, and *Taeniopteryx nivalis* (Fitch) in one year. The life cycles of *Isogenoides colubrinus* (Hagen) and *Ophiogomphus colubrinus* Selys could not be established from the present study.

Information obtained during this study suggests some possible correlations between the physical environment and the life cycles of the aquatic insects. Substrate type and food availability in the Kakisa River apparently influence the microdistribution of the species studied; and the general features of the region, especially the temperature regime and photoperiod, influence general life cycle patterns. The length of

the life cycle, time of occurrence of certain life cycle stages, and behavior of the organism are thought to be closely related to climate, with low temperatures accounting for slower development and protracted life cycles when compared to these phenomena in more southerly latitudes.

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I am indebted to Dr. Hugh F. Clifford for his thoroughness in the criticism of this manuscript and especially for his patience and supervision during my project. I wish also to thank Dr. W. E. Ricker for identifying the stoneflies and Dr. R. L. Newell for identifying the dragonfly.

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For their friendship and inspiration during the final stages of my project I owe a great debt to W. Ives, D. Simpson, J. Perreault, and my comrades at 11011-88th Ave. I am most grateful to these and other friends for challenging my philosophical perspective and sharpening my intuitive abilities.

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INTRODUCTION

During the past few decades the Canadian north has been opened up by the economic needs of man. Exploration and development have burgeoned. Starting in the 1960's, there has been growing concern over the environmental impact of these activities. This has come about largely because of an increased consciousness of man's necessary and complex relationship to the realm of Nature. As a result of this heightened awareness and subsequent concern, serious ecological investigations of human impact upon various ecosystems, and particularly the North (boreal and Arctic regions), became imperative. One general approach that has been used by environmentalists is, quite simply, the "before" and "after" schema, often in conjunction with development, sometimes with a distinct predilection toward preventing development altogether. Although my study was undertaken initially for entirely different reasons, the imminent development of a hydro-electric facility (NCPC, 1972) on a section of the Kakisa River eventually imparted a sense of urgency to the study. (At the time of this writing the NCPC proposal has not been carried out.)

Originally, my primary purpose was to provide some basic limnological information about a boreal lotic environment. I had hoped to establish a tentative and partial ecological characterization of the river by monitoring physical and chemical parameters and then correlating these with data obtained on life cycles of key members of the benthic macrofauna. This purpose, though ultimately accomplished, was changed in perspective by the proposed development of the hydro-electric facility. Although not incorporated into the body of this thesis, the possible impact of this proposed facility on the entire Kakisa drainage system, including the native Indian (Slavee) population, was a definite and pervasive consideration. The extent to which it was pervasive can be seen through perusal of other studies where the significance of environmental impact was the primary focus (e.g. Lamoureux, 1973), and where substantial ecological data on other aspects of this system were obtained (Christiansen, 1976). Although my study did not incorporate specific information concerning environmental impact, it was inspired, in part, by the relevance of such impact. All the Kakisa River studies, although each one differed in its approach, were influenced by more than biological considerations; and all must be read to comprehend the ecological dynamics of the Kakisa River drainage system.

Finally, the present study should be described as a "groundwork" project with data obtained qualitatively instead of quantitatively. That is, this study was designed to provide basic descriptive type, phenological information. Also, as a "groundwork" project, it should have value as a source of background material for more specialized research on the river system, especially with respect to the Plecoptera fauna. The project can be seen as a pilot study with the hope that it will inspire further contributions to the scientific knowledge of a northern environment.

DESCRIPTION OF STUDY AREA

Location

This study was undertaken during 1972 and 1973 within a 12 km stretch of the Kakisa River, a minor tributary of the MacKenzie River in the Northwest Territories, Canada. The relevant stretch is at latitude 60° 58' N and longitude 117° 20' W (center of study area) and is approximately 47 km south-southeast of Fort Providence, N.W.T. The river originates west of the Cameron Hills (60° N, 120° W) and flows generally in a northeasterly direction, emptying into the Beaver Lake section of the MacKenzie River (Fig. 1). Two encampments and one permanent biology station were used as bases of operation during the study period: (1) Kakisa village, a Slavee Indian village at the outlet of Kakisa Lake, (2) an old Highways Department encampment at Kakisa Crossing, approximately 3.5 km below Lady Evelyn Falls, and (3) Heart Lake Biological Station (Department of Zoology, University of Alberta), 43 km east-southeast of the study area on the MacKenzie Highway (Fig. 2).

Description of Drainage Basin

The Kakisa River has a watershed area of 14,948 sq. km and a total estimated length of 260 km, including two large lakes along its course. Most of the drainage area exhibits little relief and includes large muskeg regions. There are two prominent features, however, these being the Redknife Hills to the west, rising to 790 m (above mean sea level) and the Cameron Hills plateau to the south, rising to 880 m. Also obvious, though scarce, are various bedrock outcroppings occurring as escarpments and cataracts along rivers. The two lakes are significant

Figure 1. Map of region surrounding study area.

Key: A - study area
B - Heart Lake Biological Station

Insert map: Black circle •- study area
GSL - Great Slave Lake
MR - MacKenzie River
KR - Kakisa River
HR - Hay River

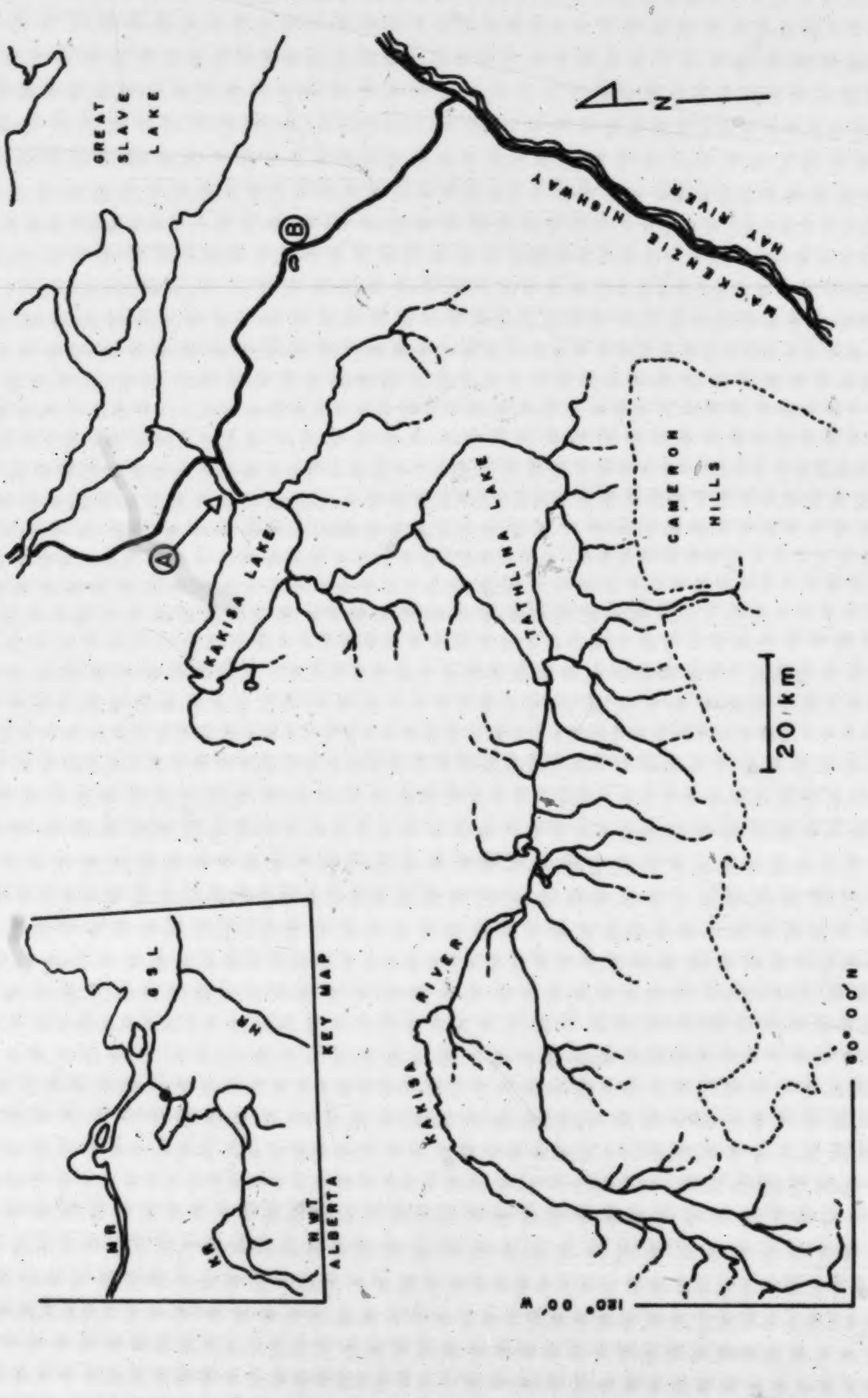
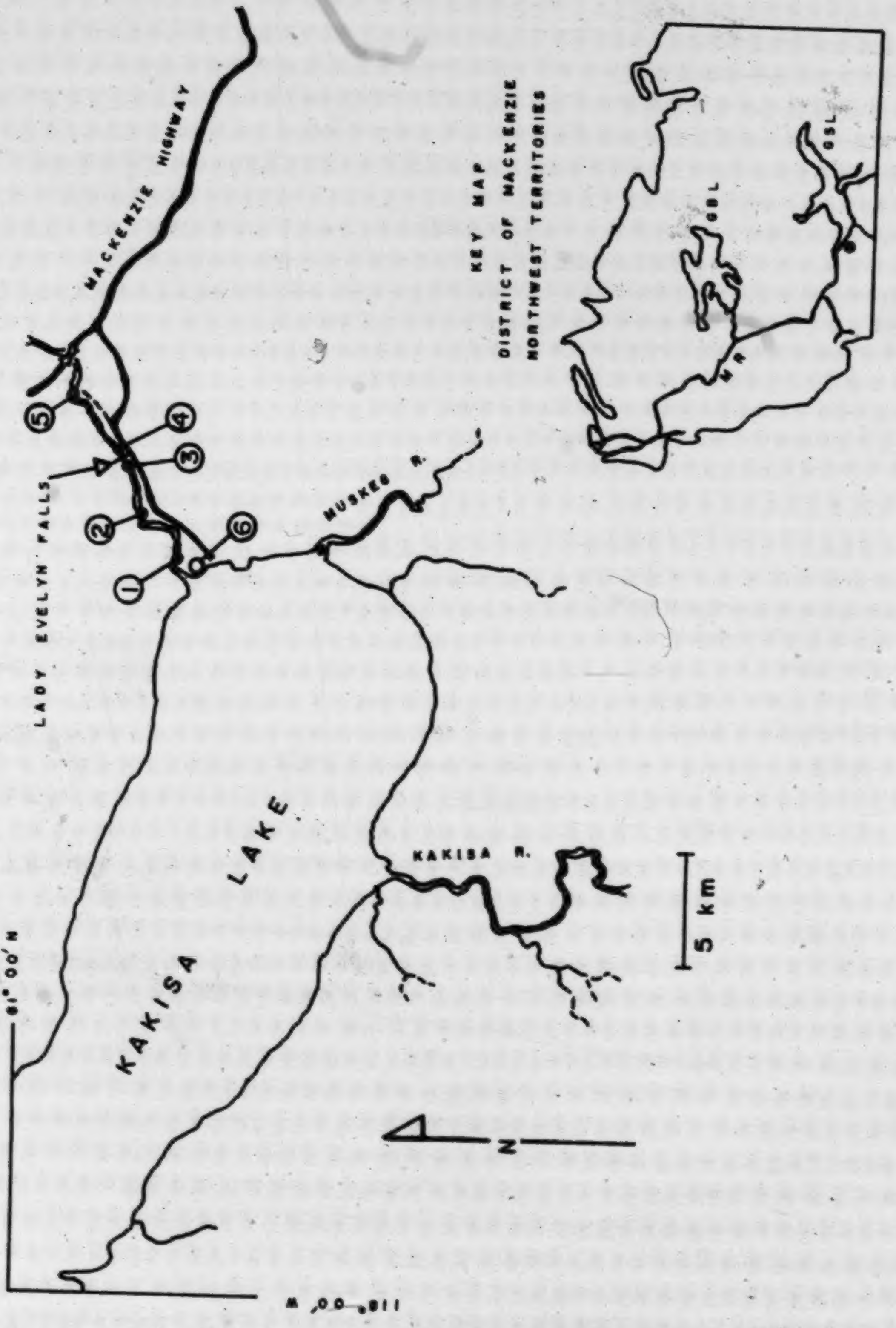

GREAT SLAVE LAKE
KAKISA LAKE
TATHLINA LAKE
CAMERON HILLS
KAKISA RIVER
MACKENZIE HIGHWAY
HAY RIVER
A
B
N
20 km
120° 00' W
60° 00' N
MR
GSL
HR
KR
NWT
ALBERTA
KEY MAP

Figure 2. Map of study area and environs

Key: 1 - 5 = stations 1 - 5
6 = Kakisa village

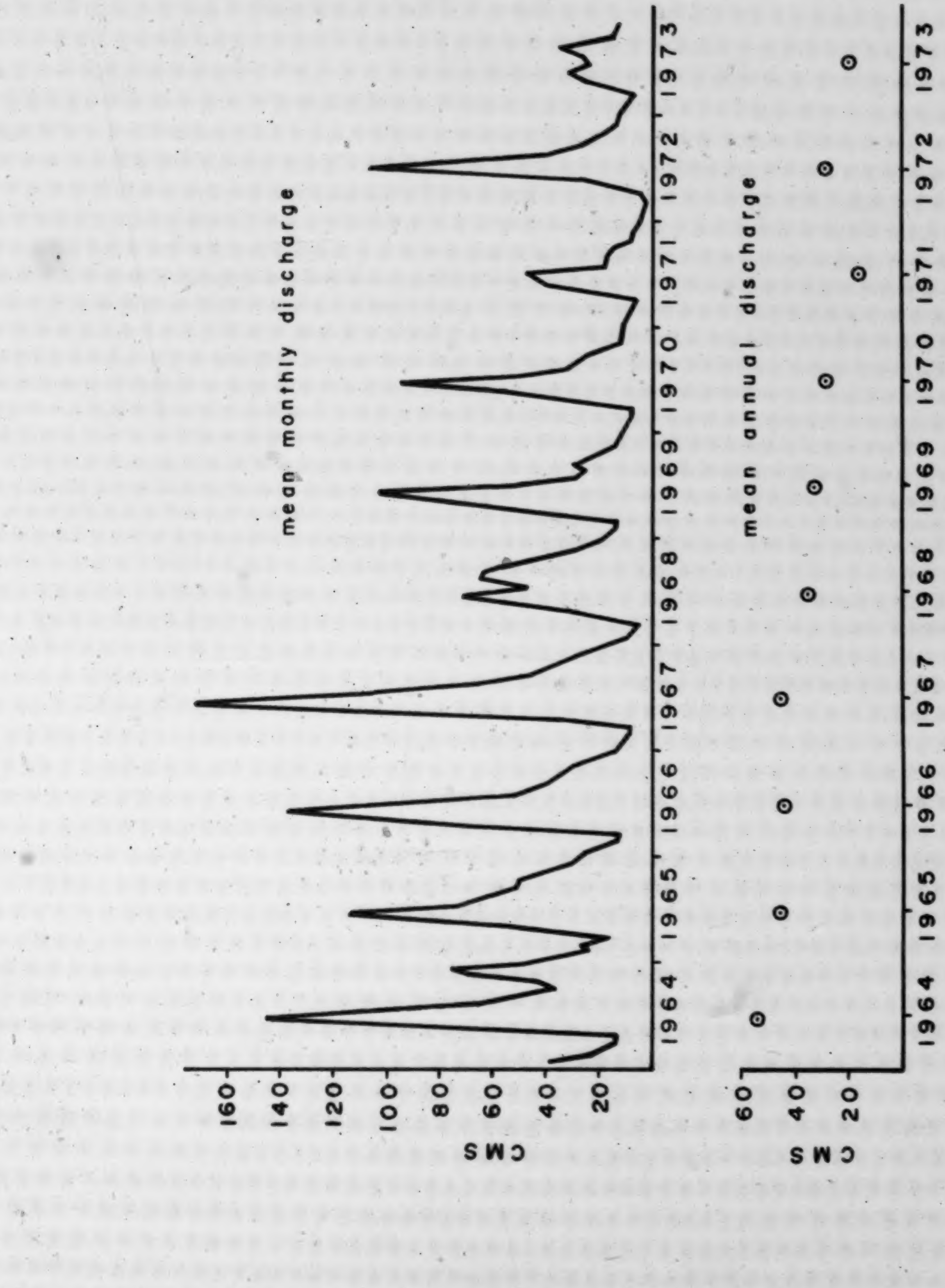
Insert map: Black circle - study area
GBL - Great Bear Lake
GSL - Great Slave Lake
MR - MacKenzie River


MACKENZIE HIGHWAY
LADY EVELYN FALLS
①
②
③
④
⑤
⑥
MUSKEG R.
KAKISA LAKE
KAKISA R.
5 km
N
61° 00' N
118° 00' W
KEY MAP
DISTRICT OF MACKENZIE
NORTHWEST TERRITORIES
GSL
GBL
M R

in the overall hydrodynamics of the river system. They have a profound influence on the temperature regime, turbidity, flow regulation, and a multitude of other parameters that will be discussed in another section. Tathlina Lake (276 m a.m.s.l.), lying parallel to the base of the Cameron Hills, is farthest upstream of the study site. It is the larger lake, being 64 km in length and having a surface area of 570 sq. km. The lake is very shallow and its littoral area is covered by rooted aquatic plants. Kakisa Lake (220 m a.m.s.l.) is immediately upstream of the study site and has a more direct impact on it. This lake is 42 km in length and has a southeasterly directional aspect, coinciding with the predominantly westerly wind flow. The lake has a surface area of about 350 sq. km and is also very shallow, with an average depth of 3.8 m. Kakisa Lake has been described as warm in the summer (18-20°C), isothermal, near-eutrophic, high in dissolved oxygen (near saturation year-round), and with a flushing period of only 1.1 years (Lamoureux, 1973). All of these factors tend to create an environment where rapid physical and chemical fluctuations are often the rule rather than the exception.

Flow regime charts for the Kakisa River show a general decline in volume of discharge between 1964 and 1973 inclusive (Fig. 3). For the study period, mean annual discharge was 29 m^3/sec. in 1972 and 20 m^3/sec. in 1973. High and low values for this period were 121 m^3/sec. in June 1972 and 2 m^3/sec. in March 1972. The water temperature regime can best be expressed by the maximum diurnal water temperature change on a monthly basis. For 1973, these values were as follows: January - (0°), February - (0°), March - (0°), April - (unknown, probably not greater

Figure 3. Mean monthly discharge and mean annual discharge of the Kakisa River, 1964—1973. Data from Inland Waters Directorate, Water Survey of Canada: CMS = cubic meters per second.


mean monthly discharge
CMS
160
140
120
100
80
60
40
20
1964
1965
1966
1967
1968
1969
1970
1971
1972
1973
mean annual discharge
CMS
60
40
20
1964
1965
1966
1967
1968
1969
1970
1971
1972
1973

than 2°C), May - (5°C), June - (7°C), July - (6.5°C), August - (6.5°C), September - (unknown), October - (unknown, probably not greater than 2°C), November - (0°), and December - (0°). During the study period, the highest and lowest recorded water temperatures were 24.5°C (July 30-31, 1973) and -0.5°C (Oct. 8, 1972). Total degree days per year was approximately 1820°C in 1972 and 2250°C in 1973. For the period 1964—1973, the average number of ice-free months per year at the study site was approximately six. "Ice-free" here refers to conditions over the body of the river and not to shoreline ice shelves or to ice floating down the river during break-up and freeze-up of the lake. Break-up in the river usually occurs between early April and early May (late May and early June for Kakisa Lake) and freeze-up between early October and early November. A short stretch of the river at the Indian village (outlet of lake) apparently remains open year-round, most likely as a result of the turbulence created by funnelling lake water into the narrow stream channel. During the study period, the stream was ice-free from 10 May to 21 October in 1972 and 11 May to 5 October in 1973.

The general stream type is erosional. Stream gradient is approximately 3 m/km, including Lady Evelyn Falls, which has a precipitous drop of 14.5 m. Estimated side slope gradient of the study area (average of ten locations: stations 1-5, north and south banks of each station) is approximately 43%. Average width of the stream is ca 30 m (study area).

Geology of the Area

The Kakisa drainage basin is part of the geological region known as the Interior Platform of northwestern North America and is a region of tectonic stability and relative geological simplicity. The Platform, lying between the orogenic belts of the Rocky Mountain Cordillera to the west and the great Precambrian Shield to the northeast, is underlain by nearly horizontal strata of bedrock of Phanerozoic origin. The Kakisa region is part of the Great Slave Plain, one of the extensive plains and plateaux that form the Interior Plains physiographic province. This province can be characterized topographically by its mantle of glacial drift; that is, the bedrock is almost totally covered by thick deposits of glacial till, giving the area a typical undulating to flat appearance with little relief and vast areas of muskeg. Where the bedrock is exposed, due to faults (scarps) and the action of rivers, it is often fractured or otherwise strongly eroded. Within the study area the outcropping of bedrock (e.g. Lady Evelyn Falls, which is part of an escarpment) and the erosional action of the river have exposed Paleozoic strata of upper Devonian origin. The underlying bedrock has limestone as its major constituent.

The Laurentide ice sheet covered this region during the (Pleistocene) Wisconsin glaciation. The area is covered, often to a depth of several meters, by both glacial and postglacial deposits: the former consist of ground moraine and other kinds of glacial drift or till; the latter consist of lacustrine deposits (e.g. beach ridges) from the glacial Lake McConnell and glacial (ancestral) Great Slave Lake. Both of these lakes apparently covered the Kakisa drainage basin as far upstream as the south shore of Kakisa Lake.

Climate

Data recorded at the Fort Providence climatological station, which is the station nearest to the study area, provide good information on the temperature and precipitation regimes between 1941 and 1970 inclusive (Atmospheric Environment Service, 1941—1970). Mean total precipitation per year for this period was 26.3 cm with a mean annual rainfall of 13.8 cm and a mean annual snowfall (not water equivalent) of 125.5 cm. Mean daily temperature per year for this period was -4.1°C with mean monthly temperatures showing a low of -26.8°C for January and a high of 16.2°C for July. More detailed meteorological information covering 1972—1973 and dealing specifically with the study area will be provided in another section.

Boreal Ecology

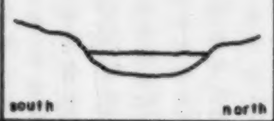
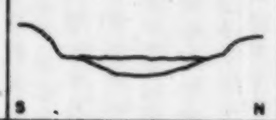
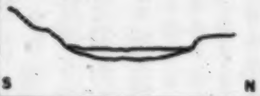
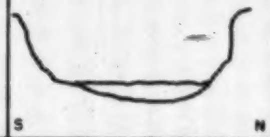
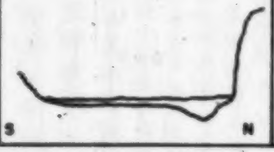
The Kakisa River lies within the Boreal Forest of northern sub-Arctic Canada. On the well-drained slopes above the river channel, the dominant tree species are white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), balsam poplar (*Populus balsamifera*), and quaking aspen (*Populus tremuloides*). The attenuate spires of white spruce are a dominant feature of the landscape, except on disturbed sites and the driest and most rocky terrain, where quaking aspen and jack pine are found. No species provides a canopy over the river itself, although the damper banks and shoreline areas are covered in part with alder (*Alnus* spp.), dogwood (*Cornus* spp.), willow (*Salix* spp.), and occasionally large trees such as spruce and poplar. The extensive muskeg regions are typified by standing water or mats of *Sphagnum* moss and other types of vegetation associated with poor drainage. Black spruce (*Picea mariana*) is the major tree species here.

The most abundant higher aquatic plants in the Kakisa River are *Potamogeton* spp. (probably *vaginatus* and *richardsonii*), being ubiquitous throughout the course of the study area and most abundant between the waterfall and Kakisa Lake. During late June, July, and early August, the abundance of *Potamogeton* at the outlet of the lake tends to have an impounding effect. Higher aquatic plants made sampling difficult in August and early May, especially at station 2 where much rotten vegetation accumulates.

Specific Sampling Sites

The study area consisted of five sampling stations along the south shoreline of the river (see Figure 2). All except station 1 were used during the 1972—1973 sampling period. Station 1 was abandoned in early 1973 because of disturbances associated with its proximity to a refuse site (I observed washed-up animal carcasses at this site). Table I compares each station using some relevant physical characteristics. One aspect of the river that was difficult to determine was the average depth over the study area. Wide seasonal fluctuations in water level coupled with inaccessibility to many deeper portions of the river, because of strong currents, made such measurements impossible. Estimated maximum depth at any station at the highest water level attained (June, 1972), however, was probably no greater than 1.8 m.

Table I: Characterization of each sampling station within the study area.

STATION	APPROX. DISTANCE FROM LAKE OUTLET	ESTIMATED RIVER WIDTH	TYPE OF SUBSTRATE*	SIDESLOPE GRADIENT AND BOTTOM PROFILE (roughly proportional)	GENERAL DESCRIPTION OF RIVER	NATURE OF STATION (how used)
1 1972 ONLY	1 mile 1·6 km	30 meters	-angular and rounded rubble -scattered large boulders -thin layer of silt and some decayed vegetation		-some exposed rubble, but current comparatively unbroken and steady -rooted aquatics prevalent in summer	- plankton samples - "kick" samples (macroinvertebrates) -water chemistry samples
2 1972 1973	2 miles 3·2 km	30 meters	-angular and rounded rubble -scattered large boulders -thin layer of silt and decayed vegetation		-bottom rubble not exposed anywhere -current steady, unbroken -rooted aquatics thick in summer	- "weather" station: max-min thermometers for air and water temp. 1973, thermohydrograph 1972 -plankton and "kick" samples -drift samples(also at lake outlet) -emergence traps; water chemistry -dock built to aid sampling -meter stick attached to dock for water level measurement
3 1972 1973	4 miles 6·4 km (immediately above waterfall)	30 meters	-bedrock -mostly angular rubble -fragmented bedrock (slabs)		-cataracts immediately above station; much turbulence -current broken somewhat by bedrock fractures and rubble	-plankton samples -"kick" samples -water chemistry samples (1972 only)
4 1972 1973	4 miles 6·4 km (immediately below waterfall)	30 meters	-rounded rubble -some riffle areas		-much turbulence below waterfall (pool) but steadier in the channel a few meters downstream -no exposed rubble	- plankton samples -"kick" samples -water chemistry samples (1972 only)
5 FROM 6/11 1972, 1973	6 miles 9·6 km (Kakisa Crossing)	100 meters	-bedrock -extensive angular rubble -riffle areas		-wide, shallow channel with small cataracts and much exposed rubble -"white water" prevalent -mats of epilithic vegetation covering bedrock in summer	-plankton samples -"kick" samples -water chemistry samples -emergence traps

*1. maximum rubble diameter approximately 100 cm, typical range 10 - 30 cm

2. run-off and wind-related turbidity cause temporary fine sediment deposition (thin layer) (stations 1 and 2)

3. decaying vegetation temporarily accumulates (thin layer of flocculents and precipitates) in summer over bottom in general and around rubble in particular (all stations)

METHODS

Various sampling procedures and methods of analysis were utilized in the field work of 1972 and 1973. What could not be accomplished *in toto* in the field was completed in laboratories at the Department of Zoology, University of Alberta, Edmonton. Information that could neither be obtained during sampling runs nor by means of complementary field work was acquired from other agencies or individuals. Although general weekly sampling runs were attempted, a variety of circumstances made regular sampling schedules very difficult to maintain. These included problems related to the peculiarities of the river, weather conditions, and the failure of experimental equipment and procedures. Sufficient sampling runs were made, however, within each of the periods of field work as follows: May 1 - August 18 and October 6 - 11, 1972; February 27 - March 3, May 1 - September 1, and October 7 - 8, 1973.

Physical

Daily, monthly and annual discharge data and information on ice conditions for the period 1963—1973 were obtained from the Inland Waters Branch of the Water Survey of Canada, Department of Energy, Mines, and Resources (Calgary, Alberta). They maintained station 7UC-1 (continuous monitoring station) on the south bank of the Kakisa River at its outlet from Kakisa Lake (Indian village) and the cable apparatus (for initial soundings) located 2 km downstream of the station.

Although the permanent monitoring station (7UC-1) recorded water levels, a meter stick adjacent to the dock at sampling station 2 also served this purpose. The meter stick provided rough indications of changes in water level during 1972.

Water temperatures were continuously recorded by means of a Ryan D-30 thermohydrograph located on the river bottom 2 m from the south bank of station 2. Use of this instrument was discontinued in mid-summer 1972 because of malfunction. Daily water temperatures were also taken using a maximum-minimum thermometer suspended below the dock at station 2 from June 19 to July 16, 1972 and from May 29 to August 28, 1973. A mercury pocket thermometer was also used during sampling runs at each station.

Daily air temperatures at station 2 were taken using a maximum-minimum thermometer from June 19 to August 13, 1972 and from May 14 to August 28, 1973. Supplementary meteorological information was obtained from data recorded at Heart Lake Biological Station, Fort Providence, and two stations in the Hay River area.

Water transparency was measured using a Secchi disc during 1972, but this was done only sporadically due to difficulties with the river current. Turbidity measurements were made with a Hach DR-EL kit. Conductance and color were ascertained from preserved samples brought [illegible]ck to Edmonton for analysis.

Chemical

Water chemistry analysis was done both in the field and in the laboratory (on preserved water samples brought back to Edmonton). Water samples were taken as regularly as possible, generally on a weekly basis. The samples that were to be sent to Edmonton were preserved with a few drops of chloroform and later frozen for extended periods until analysis could be made. All field analysis was done with a Hach DR-EL kit, with the exception of tests made for dissolved oxygen and some of the alkalinity tests. Dissolved oxygen was determined by means of the Alsterberg (Azide) Modification of the Winkler Method; total alkalinity (as $CaCO_3$) was determined using brom-cresol green indicator (Hach kit) or methylorange indicator.

Water chemistry analysis made with the Hach kit included alkalinity, calcium and total hardness, pH, turbidity, and, less regularly, iron, silica, and manganese. Laboratory analysis of preserved samples included alkalinity, calcium and total hardness, pH, turbidity, color, total dissolved solids (residue), iron, silica, chloride, sulfate, orthophosphate, and nitrate nitrogen. Preserved samples were sent to the Water Analysis Laboratory, Department of Zoology, University of Alberta, where "Standard Methods" (A.P.H.A., 1971) were used in all analyses.

Biological

General

Bottom fauna samples were collected at each station once per week to once every two weeks, and newly emerged adults were collected daily from traps at two stations. Preservation and partial sorting of samples were done in the field on the day that the samples were collected; final sorting was carried out in the Edmonton laboratory. The preserved and sorted samples were analyzed in Edmonton. Plankton and drift samples were taken regularly but they have not been analyzed. Difficulties with sampling procedures and interpretation — and ultimately lack of time and altered priorities with respect to the intentions of this project — did not allow a more complete analysis of these and related data. Such data could have provided drift, species composition and other complementary information, but these were not considered essential to the primary purpose of the study. This thesis, therefore, is concerned primarily with life cycle determinations based solely upon the information obtained from the bottom fauna and emergence samples.

Collecting Procedures

During each sampling run at each station both plankton and bottom samples were taken. The plankton samples were obtained with a Japanese (Kyoto) plankton net 24.9 cm in diameter, 44.9 cm in length and having a mesh size of 76 microns. The net, attached to a rope 4.7 m in length, was thrown downstream and pulled back three times, the material being preserved in 10% formalin. Bottom samples (primarily for Ephemeroptera and Plecoptera nymphs) were taken using the "kick" method (Frost, Huni and Kershaw, 1971). Three samples were collected using a double net and preserved in 10% formalin, the inside net of 1 mm pore size and the outer net, detachable by means of a zipper, of 126 micron pore size. A fourth sample was taken with a single net of 1 mm pore size and deposited in the same container. The single net was used in areas where stronger currents made use of the double net, or even a fine-meshed single net, impossible. Each of the four "kick" samples was accomplished in approximately 5 minutes.

In 1972 several attempts were made to collect emerging adult Plecoptera and Ephemeroptera with a variety of traps, all of which proved unsuccessful. Some of the traps were designed for use on the river bottom, some for the water column, and some for floating on the surface. Floating debris and rapid changes in water level damaged the traps and many were lost or completely destroyed. No exuviae were collected regularly and shoreline traps were not employed in 1972.

In 1973, open-water and shoreline traps, both of original design, were employed at two stations (Figs. 4 and 5). Two of the open-water traps were suspended in the surface current 5 m from the south shoreline at station 2 on May 29 and a third was added on June 11; all were removed June 27 after many attempts at keeping them free of floating debris and adjusting them to changing water levels proved unsuccessful. These traps did not collect any adult ephemeropterans observed floating on the river and emerging onto the surface of the river, although traps were checked daily and adjusted frequently.

Three shoreline traps with the open ends projecting approximately 15 cm into the water were weighted down 7 m apart at the shoreline of station 2 on May 18. Three traps were set in a similar fashion at station 5 the same day. On June 27 one trap was lost from station 2 and replaced with two of the old open-water traps, the open end of an open-water trap being one half the width of the open end of a shoreline trap. The 7 m distance between each trap was subsequently maintained. All traps were checked daily, the contents (if any) preserved in 98% ethyl alcohol, and position adjustments made whenever the water level changed. These traps were successful in capturing odonate and plecopteran nymphs. The traps were removed on August 6, 1973.

Drift samples were collected over one 24-hour period once each week throughout the study periods of 1972 and 1973. Nets were suspended

Figure 4. Design of the emergence traps.

Key: a - hole for attachment of collecting bottle
b - slot over which collecting bottle is placed
c - holes through which support rods are placed (for attachment to poles in substrate)

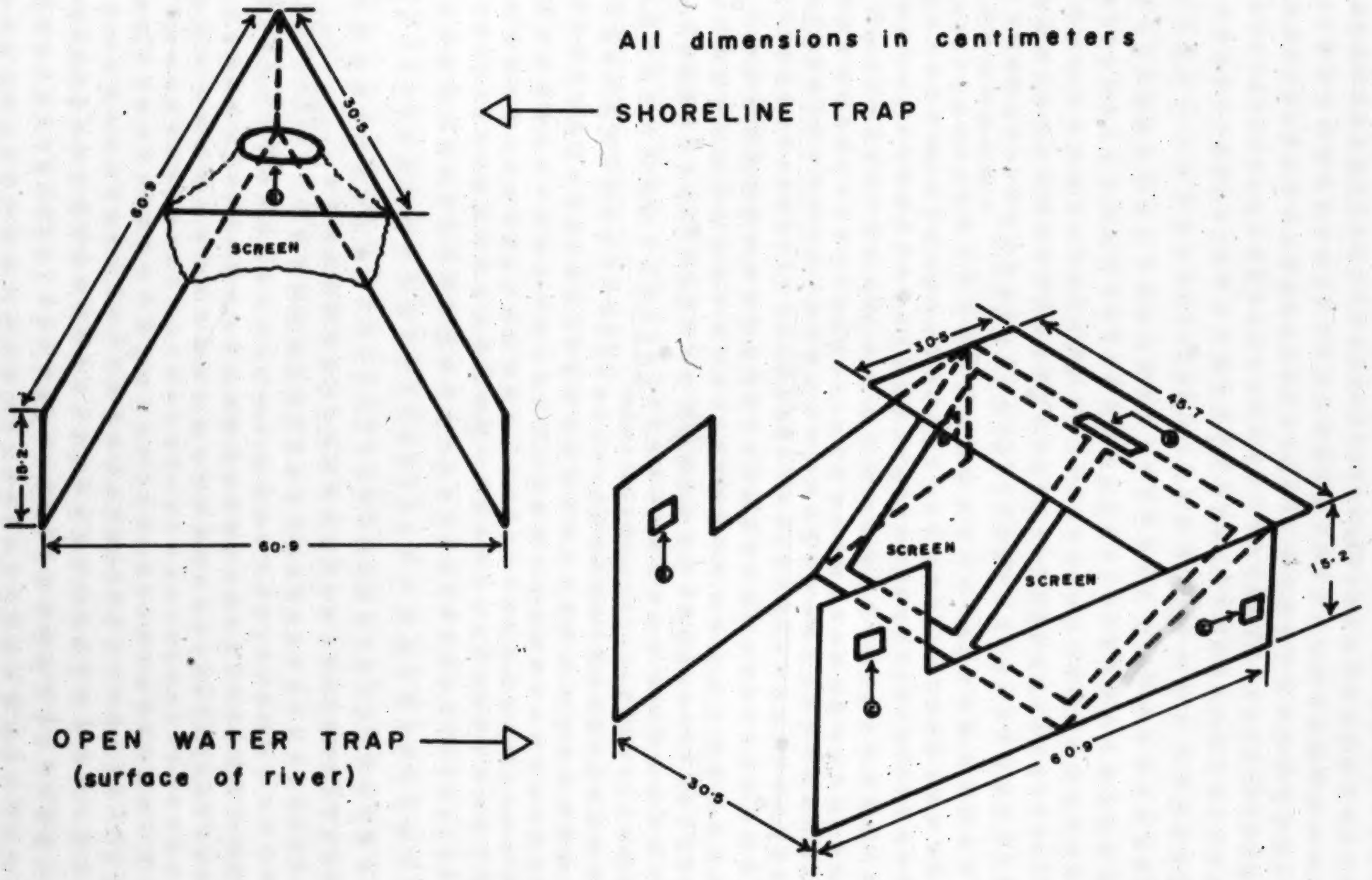
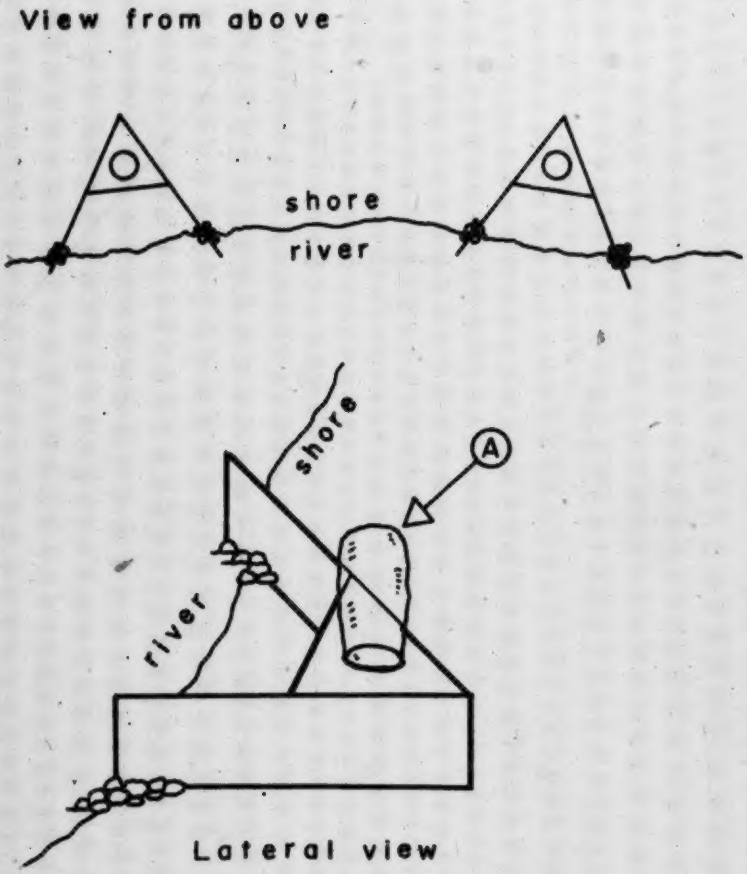
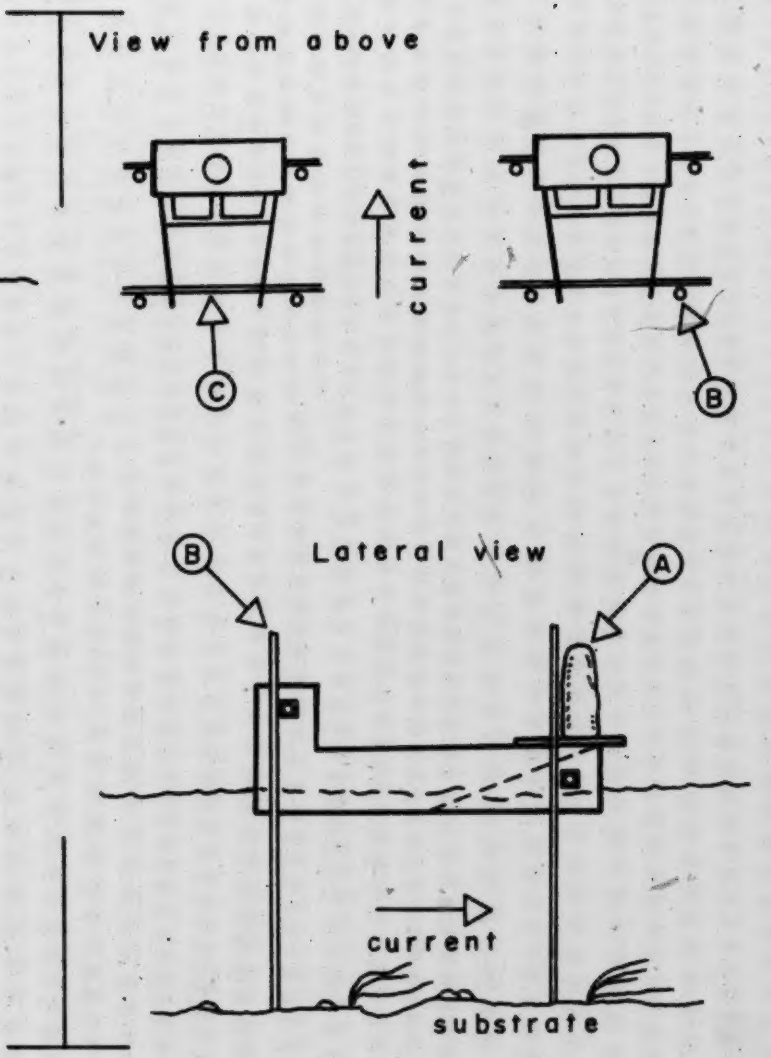

All dimensions in centimeters
SHORELINE TRAP
OPEN WATER TRAP
(surface of river)
SCREEN
SCREEN
SCREEN
60·9
30·5
15·2
60·9
30·5
45·7
15·2
60·9
30·5

Figure 5. Placement of shoreline emergence traps (left) and open-water emergence traps (right) in 1973.

Key:
- A - collecting bottle
- B - poles in substrate to which traps are attached
- C - rods through trap for attachment to poles in substrate


View from above
shore
river
shore
A
river
Lateral view


View from above
current
C
B
Lateral view
B
A
current
substrate

Diagrams not to scale

midway in the water column both at station 2 and immediately below the outlet of Kakisa Lake and were located as far out into the river channel at both sites as depth and current would allow. The samples from the outlet location were taken between May 8 and August 13, 1972, May 12 and August 22, 1973, and October 7 and 8, 1973; those from station 2, between June 11 and August 13, 1972, May 12 and August 22, 1973, and October 7 and 8, 1973. The nets used at the outlet location consisted of a double-net arrangement: a standard Surber net (1024 micron pore size, 30.5 cm^2 aperture) with fine netting (126 micron pore size) attached directly behind it and partly surrounding it. The nets used at station 2 consisted of two standard drift nets (320 micron pore size, 9 cm^2 aperture) in 1972 and one of these nets in 1973. All nets were held midway in the water column by being firmly tied to metal poles hammered into the substrate. At the end of each 24-hour period, the contents of the nets from each site were washed into large jars and preserved in 10% formalin.

Bottom fauna samples that were initially preserved in 10% formalin were later rinsed through a 126 micron screen to concentrate the organisms and then preserved in 98% ethyl alcohol. All emergence samples were directly preserved in 98% ethyl alcohol in the field.

Analysis

The bottom samples, having been preserved and partially sorted in the field, were brought back to Edmonton where sorting was completed in the laboratory. Only Plecoptera, Ephemeroptera and Odonata were picked out of the samples for further study. A fine metal screen (420 micron pore size) was used to remove sand and silt from many of the samples, quite probably having the effect of removing very small nymphs as well. For purposes of this study, only nymphs 1 mm in length and larger were used in the analysis.

When sorting of bottom samples was completed, the nymphs were identified, counted, sexed (when possible), measured, and characterized as to relative maturity. Determination of gender was impossible for the early instars of the larger species (i.e. *Pteronarcys dorsata*, *Ophiogomphus colubrinus*, and *Ephemera simulans*) and for all specimens of the small species *Isoperla transmarina*. Total length was measured to the nearest millimeter, the distance being from the tip of the head to the end of the last abdominal segment. Shape and coloration of the meso- and meta-thoracic wing pads served as the criteria for nymphal maturity and was the best indication of impending emergence. A nymph with large, acutely-angled and strongly darkened wing pads in which the venation had become apparent was judged to be in the last nymphal instar and ready to emerge.

Emergence samples needed no preliminary sorting. Adults were identified, counted, sexed, and measured (total length). And from these data, histograms of the numbers of males and females that emerged per day were constructed. Measurement of total length of adults was made in the same fashion as it was for the nymphs.

PHYSICAL AND CHEMICAL CHARACTERISTICS

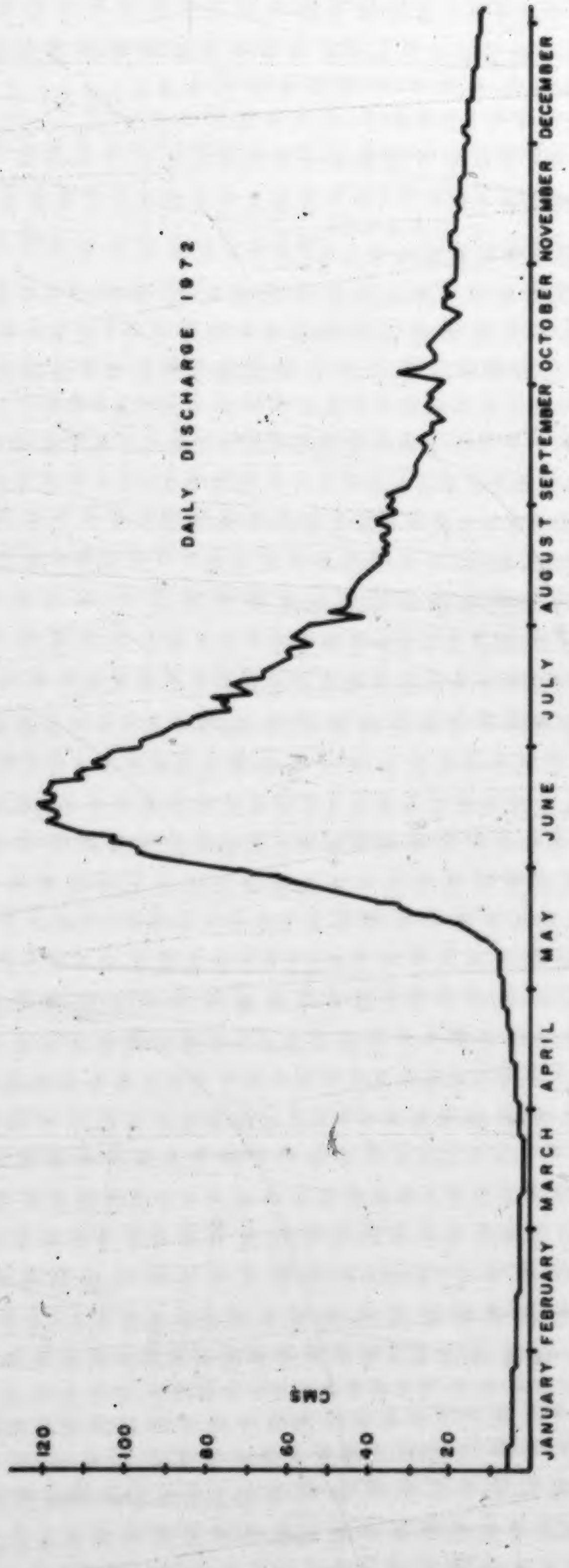
Discharge

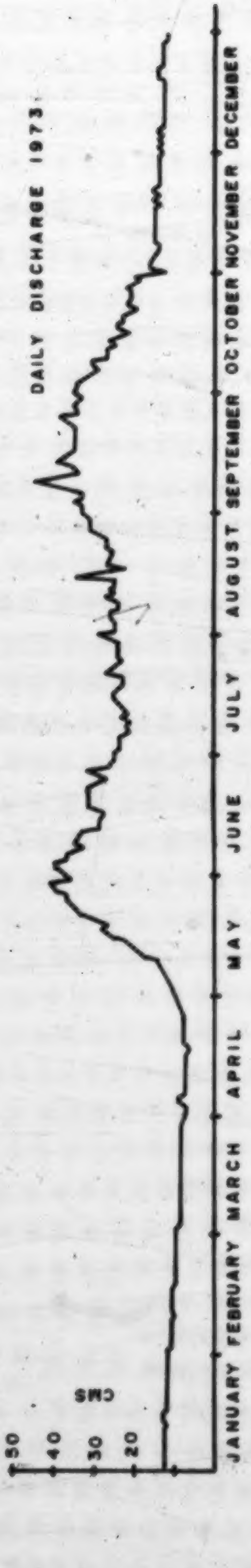
With the exception of 1972, there has been a general decline in discharge volume from 1964 through 1973 (Fig. 3). In 1972 the mean annual discharge was 29 m^3/sec., with a low of 2 m^3/sec. in March and a high of 121 m^3/sec. in mid-June. In 1972 discharge rose steadily from May 10 to the middle of June. From June 21 to August 1, the water level dropped quickly, and thereafter there was a steady decrease in flow through the end of the year (Fig. 6). The uniform, steady nature of the rise to and decline from one discharge peak to another correlates well with meteorological conditions. High discharge in June follows break-up on Kakisa Lake quite closely, and the consistently warm, dry weather throughout much of the summer (coupled with a decrease in run-off) is reflected in the evenness of the subsequent steady decline in discharge.

In 1973 the mean annual discharge was 20 m^3/sec., with a low of 7 m^3/sec. in April and a high of 45 m^3/sec. in early September. In 1973 two discharge peaks occurred, one from May 26 to June 5, which followed break-up on Kakisa Lake, and the other from September 4 to October 1, which was an indirect reflection of weather conditions (summer precipitation occurring as increased run-off in September). In general, the rise to and decline from the peaks were steady, with highs of 41 m^3/sec. and 45 m^3/sec. achieved on May 29 and on September 9, respectively (Fig. 6).

Seiche conditions in Kakisa Lake appeared to be frequent during the summer months and seemed to have some influence on the study area of the

Figure 6. Daily discharge of the Kakisa River in 1972 and 1973. Data from Inland Waters Directorate, Water Survey of Canada.


DAILY DISCHARGE 1972
CMS
120
100
80
60
40
20
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER

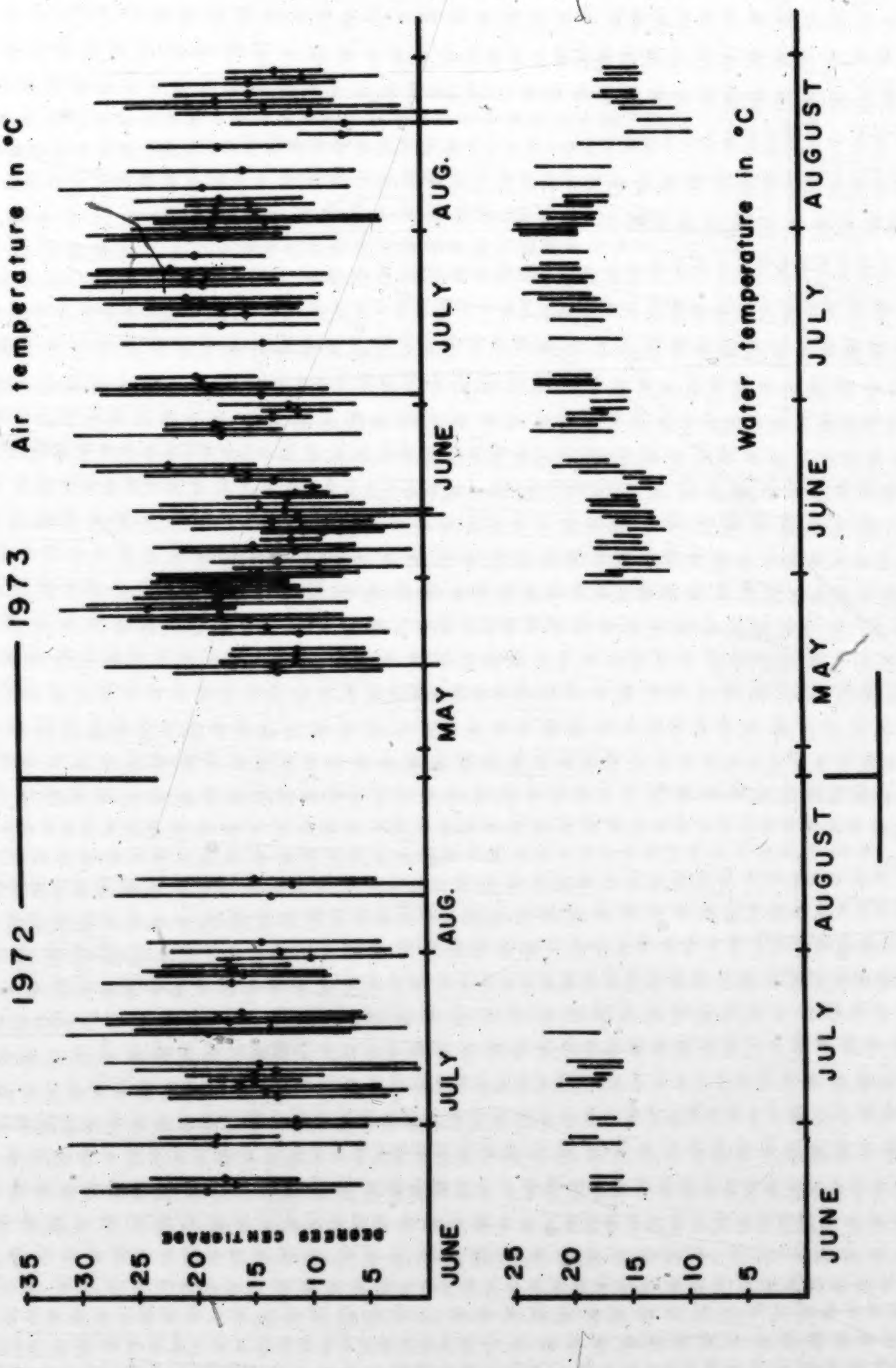

DAILY DISCHARGE 1973
CMS
50
40
30
20
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER

river. Although continuous recordings of water level were made (Inland Waters Branch) and large fluctuations observed, especially after storms and high winds or both, records of seiche data were not available. Dramatic and regular fluctuations of at least several centimeters per hour have been observed during and immediately after storms, indicating the prevalence of seiches. The shallowness of the lake, the frequency of high winds of variable duration blowing from the west directly down the length of the lake, plus the general morphometry of the lake (long, relatively narrow, and sufficiently regular in shape) all contribute to the frequent and pronounced incidence of seiches. Seiches in Kakisa Lake must account for rapid and substantial changes in the turbidity, discharge, temperature, and related features within the study area of the river.

Temperature

Wide daily fluctuations in air temperature were common in both years, with temperatures often dropping near 0°C during summer nights and rising to the low 30's during the day (Fig. 7). A maximum daily variation of 29°C occurred on May 15, 1973; but usually variations of 20°C or less were much more common. A maximum daily fluctuation in water temperature of 7°C occurred in June, 1973, but variations of about 5°C were more common. The general trend in water temperatures for both years indicated low temperatures, often near 0°C, until the lake ice was completely gone in May, rapid warming throughout the summer to a maximum in July, and cooling to 0°C through September and October.

Figure 7. Maximum and minimum daily air and water temperatures at station 2, 1972 and 1973. Small black circles (●●●●) represent median daily air temperatures.


1972
1973
Air temperature in °C
DEGREES CENTIGRADE
35
30
25
20
15
10
5
JUNE
JULY
AUG.
MAY
JUNE
JULY
AUG.
Water temperature in °C
25
20
15
10
5
JUNE
JULY
AUGUST
MAY
JUNE
JULY
AUGUST

Turbidity

Variations in turbidity seemed more closely associated with turbulence in the lake than to river turbulence (Fig. 8). I found no apparent direct relationship between discharge and turbidity, although levels of turbidity were more variable in 1973, perhaps reflecting the more frequent fluctuations in discharge that year. Turbidity measurements made in the field yielded values that were usually less than those obtained from preserved samples in the laboratory, even though a Hach kit was used both in the field and laboratory to measure turbidity. Possibly in the laboratory, there was a loss of buffering capacity in the preserved samples, assuming CO_2 in solution was driven off when the samples were frozen and then warmed to lab temperatures (usually above ambient water temperature when the sample was taken). This would cause the bicarbonate present to dissociate and finally yield $CaCO_3$, which in turn would precipitate out as a suspension and thereby increase turbidity. It is not known whether the use of chloroform for the initial preservation of the water samples could somehow increase turbidity in the samples. But one would expect that chloroform would prevent biological activity in the samples and hence would not cause alteration in turbidity of the sample.

Conductance

Specific conductance was generally lower in 1973 than in 1972 (Fig. 9). In 1973, values rarely exceeded 300 micro-mhos. Measurements of conductance are often correlated with measurements of total dissolved solids (or total residue), which includes unfiltered material in

Figure 8. Chemical and physical features: pH, color (platinum units), and turbidity (Jackson turbidity units).

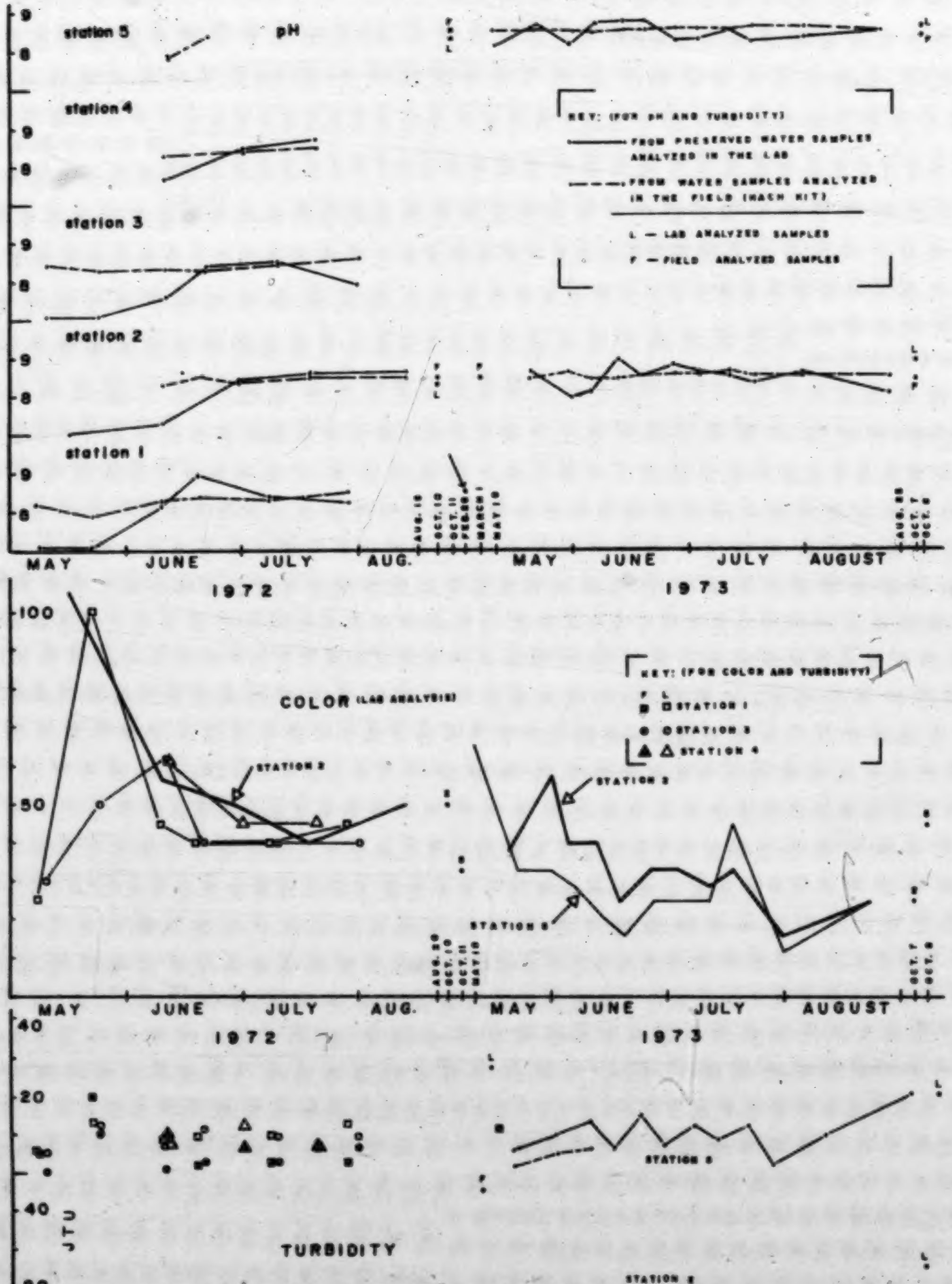
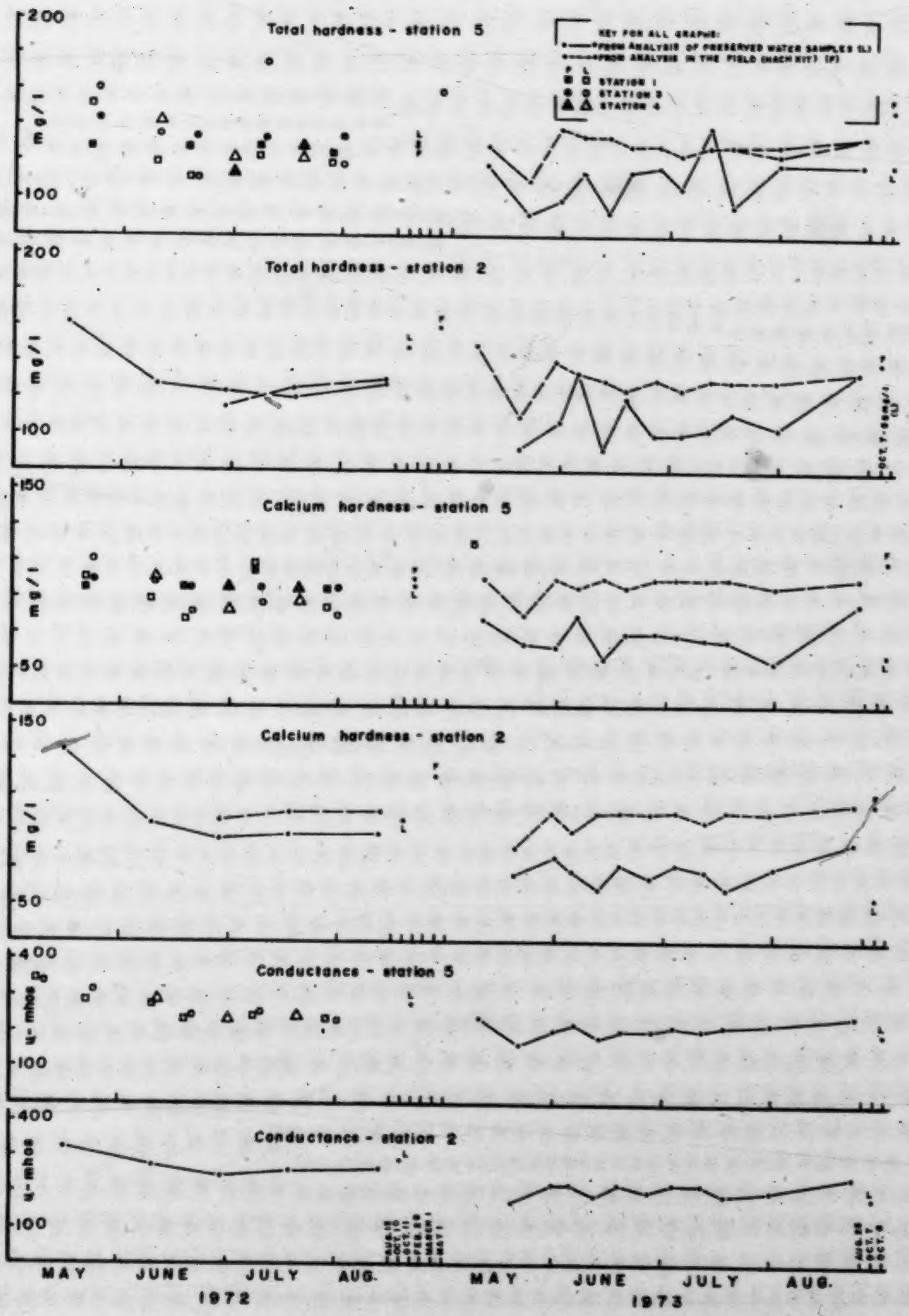

station 5
pH
station 4
station 3
station 2
station 1
9
8
KEY: (FOR pH AND TURBIDITY)
FROM PRESERVED WATER SAMPLES ANALYZED IN THE LAB
FROM WATER SAMPLES ANALYZED IN THE FIELD (HACH KIT)
L — LAB ANALYZED SAMPLES
F — FIELD ANALYZED SAMPLES
L
F
AUG. 18
OCT. 13
OCT. 11
FEB. 28
MARCH 1
MAY 19
AUG. 28
OCT. 7
OCT. 8
MAY
JUNE
JULY
AUG.
AUGUST
1972
1973
100
50
COLOR (LAB ANALYSIS)
KEY: (FOR COLOR AND TURBIDITY)
F L
■ □ STATION 1
● ○ STATION 3
▲ △ STATION 4
STATION 2
STATION 3
40
20
JTU
TURBIDITY
STATION 3
STATION 2

Figure 9. Chemical and physical features: calcium hardness, total hardness, and conductance.


Total hardness - station 5
KEY FOR ALL GRAPHS:
FROM ANALYSIS OF PRESERVED WATER SAMPLES (L)
FROM ANALYSIS IN THE FIELD (HACH KIT) (F)
F L
■ □ STATION 1
● ○ STATION 3
▲ △ STATION 4
200
100
mg/l
F
L
Total hardness - station 2
200
100
mg/l
Calcium hardness - station 5
150
50
mg/l
Calcium hardness - station 2
150
50
mg/l
Conductance - station 5
400
100
μ-mhos
Conductance - station 2
400
100
μ-mhos
MAY
JUNE
JULY
AUG.
1972
MAY
JUNE
JULY
AUG.
1973

suspension. It should therefore not be correlated with conductance. Because conductance is dependent upon the concentration of dissolved salts, its relationships to discharge, biological activity, alkalinity, other ions present, and turbidity is important. But the relationship among all these constituents is complex in lotic environments, and definite correlations are impossible. However, conductance did seem to follow changes in total alkalinity at stations 2 and 5 in 1973. Although possibly coincidental, this situation seems logical since alkalinity is a measurement of carbonates, bicarbonates, and even hydroxyl ions in solution.

Color

There was a general decrease in true color during the summers of both years and there were distinct peaks in late May and early June of 1972 and in early and late May of 1973 (see Fig. 8). Smaller peaks also occurred in mid July, 1973. The high color values apparently are due to run-off from melting snow in the surrounding terrain; this run-off would contain colloidal organic matter and inorganic solutes, substances known to impart color to running water. Although run-off from melting snow and possibly from rain was probably the major factor affecting color, turbidity might also be important. The precise relationship among these and other features remains unknown.

Dissolved Oxygen

Graphs of dissolved oxygen show rough but nevertheless typical trough-shaped curves for both 1972 and 1973 and indicate that the river always contains ample oxygen (always above 8 mg/l and 90% saturation, Fig. 10). Percent saturation follows dissolved oxygen curves fairly closely, although the percent saturation curve is somewhat inverted when compared to dissolved oxygen values of 1973. For station 2 in 1972 and 1973, dissolved oxygen and percent saturation ranged from 9 - 12 mg/l and 90 - 130%; for station 5, from 8 - 11 mg/l and 95 - 115%. Maximum dissolved oxygen and percent saturation values attained during the study period were 13.9 mg/l and 133%, and minimum values were 8.2 mg/l and 89%. Dissolved oxygen was near or above 100% saturation most of the time. This certainly represents a healthy situation as far as organisms are concerned.

Hydrogen Ion

Measurements of hydrogen ion concentration made in the field show a very stable pH of about 8.5 at all stations throughout 1972 and 1973 (see Fig. 8). The values indicate a well-buffered system resulting from complex interactions among the carbonates from limestone substrata and glacial till, acid run-off from surrounding muskeg terrain, biological activity (especially the photosynthetic process of the rooted aquatic plant, *Potamogeton* sp.), temperature, and to a lesser extent, discharge and turbidity.

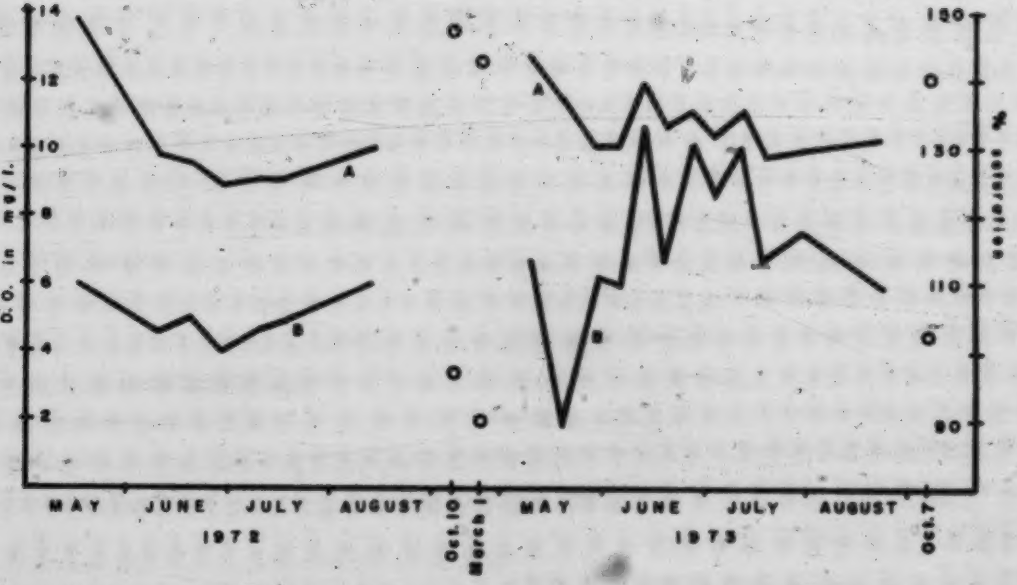
Alkalinity and Hardness

As was the case with some other constituents (e.g. pH), there was a discrepancy between alkalinity and hardness measurements made in the field and those derived from preserved samples (Fig. 11, see Fig. 9).

Figure 10. Dissolved oxygen at stations 2 and 5; small circles (o) represent specific sampling dates.

DISSOLVED OXYGEN, IN MG/L (A) AND AS % SATURATION (B)

STATION 2



STATION 5

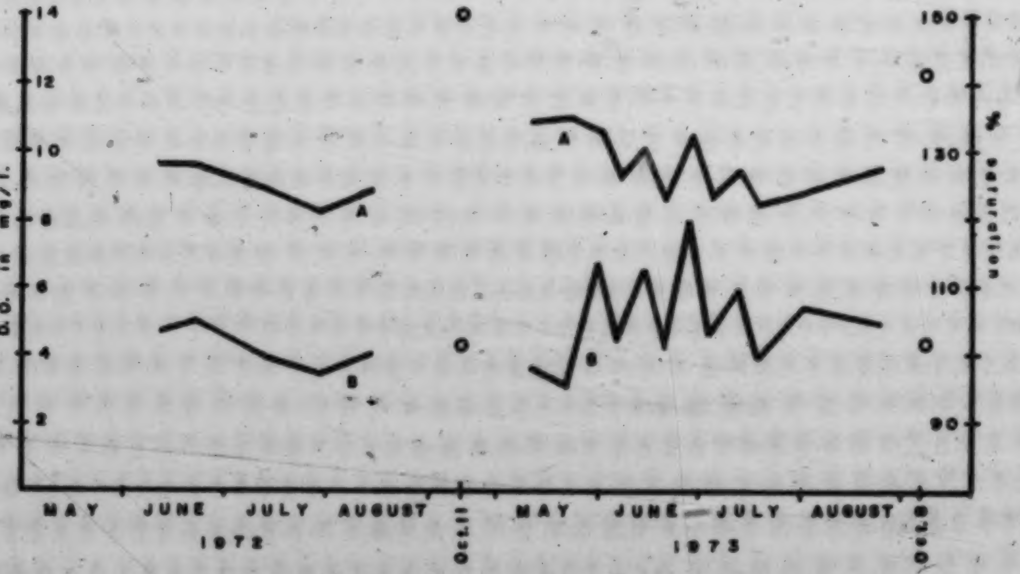
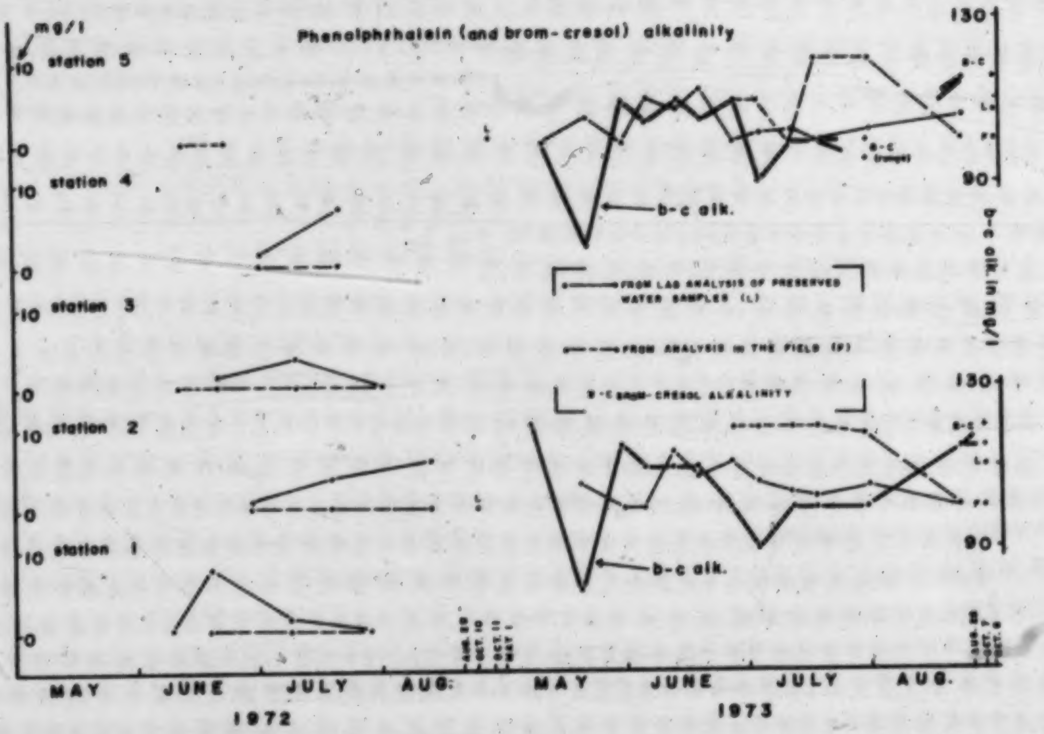
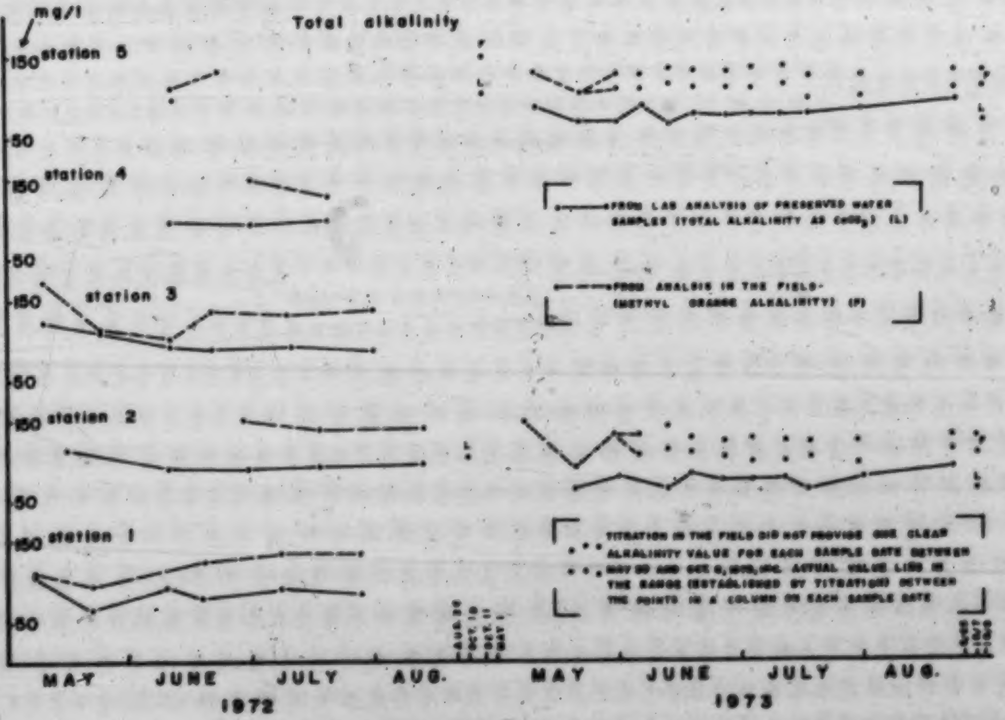


Figure 11. Chemical features: phenolphthalein and total alkalinity.


Phenolphthalein (and brom-cresol) alkalinity
mg/l
10
station 5
0
10
station 4
0
10
station 3
0
10
station 2
0
10
station 1
0
130
90
130
90
b-c alk. in mg/l
b-c
L
F
b-c (range)
b-c alk.
b-c alk.
FROM LAB ANALYSIS OF PRESERVED WATER SAMPLES (L)
FROM ANALYSIS IN THE FIELD (F)
B-C BROM-CRESOL ALKALINITY
MAY
JUNE
JULY
AUG.
1972
MAY
JUNE
JULY
AUG.
1973

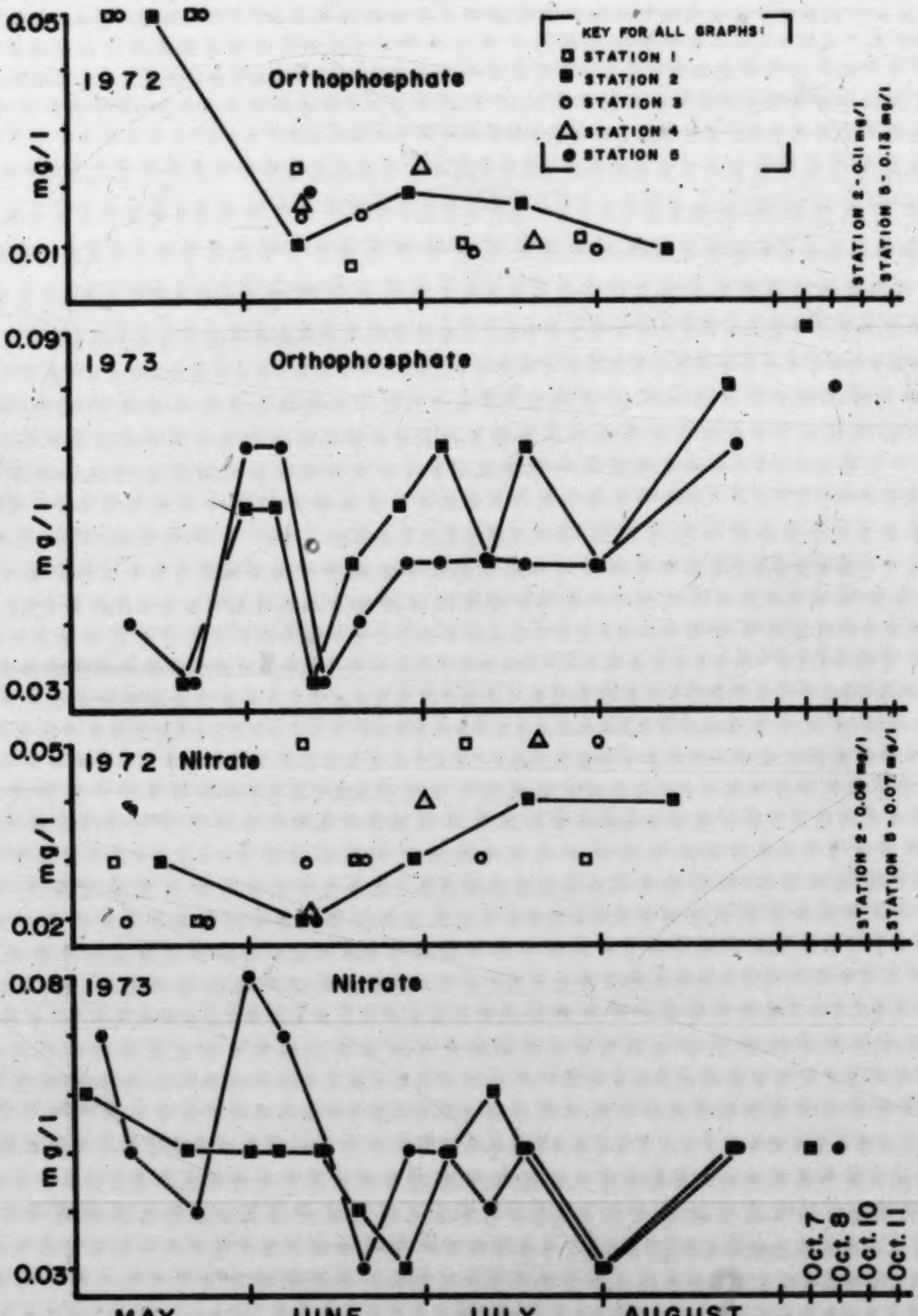

Total alkalinity
mg/l
150
station 5
50
150
station 4
50
150
station 3
50
150
station 2
50
150
station 1
50
F
L
FROM LAB ANALYSIS OF PRESERVED WATER SAMPLES (TOTAL ALKALINITY AS CaCO3) (L)
FROM ANALISIS IN THE FIELD- (METHYL ORANGE ALKALINITY) (F)
TITRATION IN THE FIELD DID NOT PROVIDE ONE CLEAR ALKALINITY VALUE FOR EACH SAMPLE DATE BETWEEN MAY 30 AND OCT 6, 1973, INC. ACTUAL VALUE LIES IN THE RANGE (ESTABLISHED BY TITRATION) BETWEEN THE POINTS IN A COLUMN ON EACH SAMPLE DATE
MAY
JUNE
JULY
AUG.
1972
MAY
JUNE
JULY
AUG.
1973

However, the graphs derived from laboratory data roughly follow the same trends as those derived from field measurements. As is characteristic of rivers flowing over limestone, the Kakisa River has moderately high alkalinity and hardness with calcium salts as the major component of both constituents. There was a close relationship between alkalinity and hardness, both showing lower values during the summer, higher values in the early spring, fall, and winter. These patterns probably reflect the influence of biological activity, especially the photosynthetic processes of rooted aquatic plants and other submerged vegetation, yet complicated by variable meteorological and hydrological conditions, especially in 1973. No measurable hydroxide was indicated by the phenolphthalein tests, which in combination with methyl orange or brom-cresol tests indicate the relative proportions of hydroxide, bicarbonate, and carbonate of total alkalinity. All tests (including measurement of pH) do indicate, however, that the photosynthetic process is probably quite significant with respect to the river as a buffered system.

Other Ions

There was a general increase in nitrate nitrogen in 1973 over 1972, with quantities falling between 0.02 and 0.08 mg/l during the two-year period (Fig. 12). On the whole, the quantities of nitrate nitrogen seemed quite low, perhaps as a result of uptake by aquatic vegetation and other unknown factors. Orthophosphate values were generally higher in 1973 than in 1972, with quantities falling between 0.006 and 0.13 mg/l during the two-year period (Fig. 12).

Figure 12. Chemical constituents: orthophosphate and nitrate.


KEY FOR ALL GRAPHS:
□ STATION 1
■ STATION 2
○ STATION 3
△ STATION 4
● STATION 5
1972
Orthophosphate
0.05
0.01
mg/l
STATION 2 - 0.11 mg/l
STATION 5 - 0.12 mg/l
1973
Orthophosphate
0.09
0.03
mg/l
1972 Nitrate
0.05
0.02
mg/l
STATION 2 - 0.08 mg/l
STATION 5 - 0.07 mg/l
1973
Nitrate
0.08
0.03
mg/l
MAY
JUNE
JULY
AUGUST
Oct. 7
Oct. 8
Oct. 10
Oct. 11

Iron was present in consistently low quantities, ranging from 0.07 to 1.37 mg/l (Fig. 13). Field values for iron were almost always lower than those obtained from preserved samples. The relationship between iron and other chemical and physical features, particularly the determinants of its chemical form and quantity at any point in time, is unknown.

Silica (as silicate or silicic acid) was found in consistently low quantities, ranging between 1.90 and 3.75 mg/l, during 1972 and 1973 (Fig. 13). Fluctuations were minimal, with somewhat lower values obtained during June and early July of both years. Lower levels during summer months might be explained in part by the uptake of silica by diatoms.

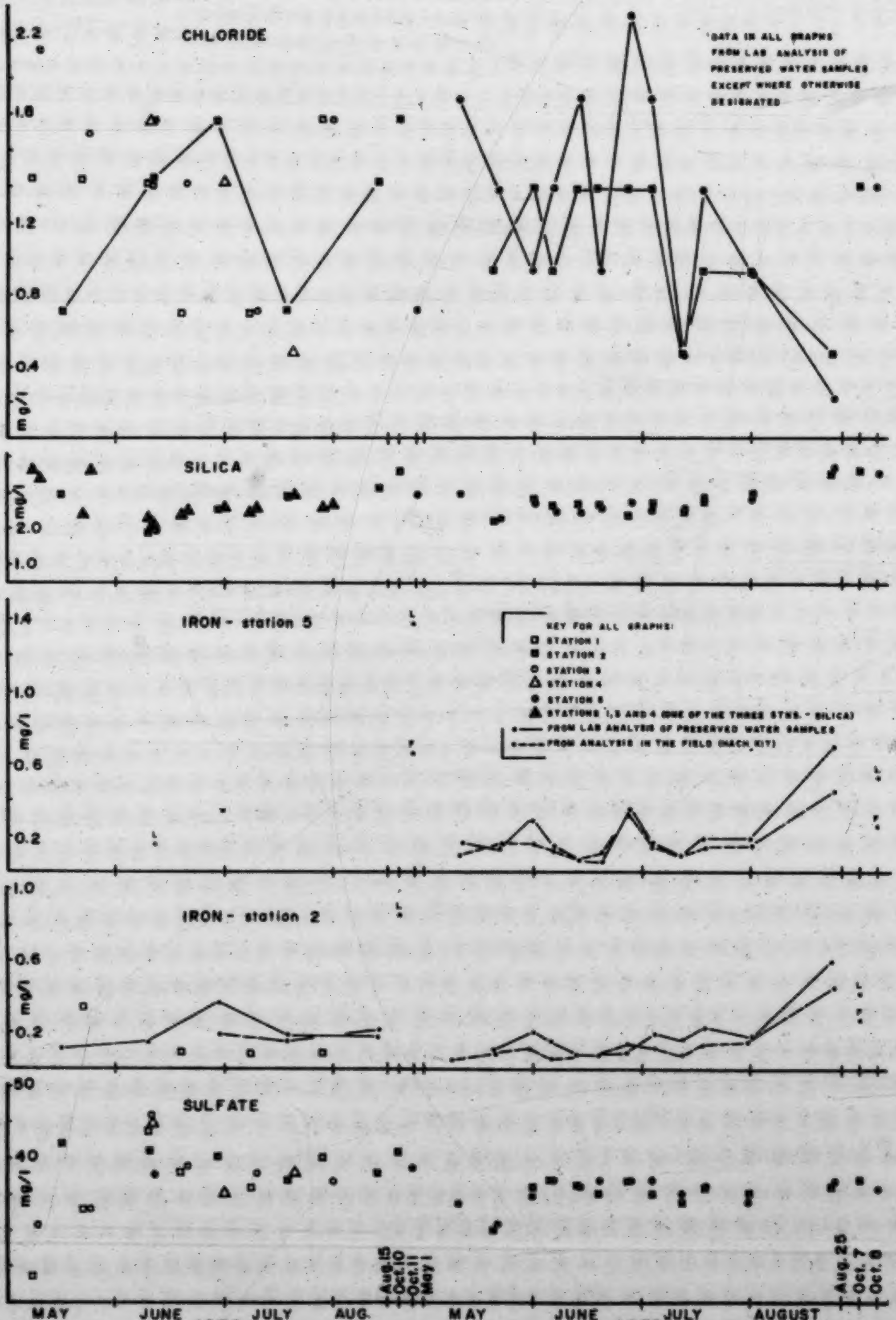
Values for chloride fluctuated between 0.21 and 2.34 mg/l during the two years of the study (Fig. 13). No consistent pattern could be ascertained; there were widely different values obtained at each station for any given period.

Sulfate levels ranged from 24 to 46 mg/l during the 2-year period (Fig. 13). The lowest values were obtained immediately prior to the seasonal increase in discharge each year. In 1972, the maximum value coincided with maximum discharge. Levels remained relatively constant throughout the summer, showing no obvious pattern with respect to other features.

Effect of Kakisa Lake on the River's Water Chemistry

Values for certain chemical and physical features obtained from the five stations of the study area and two sampling sites above Kakisa

Figure 13. Chemical constituents: chloride, silica, iron, and sulfate.



DATA IN ALL GRAPHS FROM LAB ANALYSIS OF PRESERVED WATER SAMPLES EXCEPT WHERE OTHERWISE DESIGNATED

Lake are shown in Table II. These values, obtained between June 3 - 18, 1972, show that the two sites above the lake obviously differ from all five stations downstream with respect to almost all constituents and especially to color and turbidity. Kakisa Lake has a pronounced effect on the water chemistry and physical features of several kilometers of the river downstream of the lake. During periods of high water, Kakisa Lake must moderate the effects of runoff in the stretch immediately downstream, as indicated by pH, alkalinity and color values.

Table II: River water chemistry above and below Kakisa Lake; the waterfall above the lake is approximately 5 km from the mouth of the river at the lake. All quantities are in mg/l except for pH, conductance (micromhos), color (platinum color units), and turbidity (JTU).

	pH	total alkalinity	orthophosphate	silica	nitrate-N	conductance	iron	color	turbidity	Calcium hardness	total hardness	Chloride	sulfate
June 3 mouth of river at lake	7·5	87·2	0·07	2·5	0·02	270	1·02	50	14	100	136	1·77	45
June 4 mouth of river at lake	7·55 8·2	68·9 90	0·15	1·1 3·2	0·02	230	2·0 1·2	80	39 130	88 90	120 115	0·71	39
June 8 falls above lake	7·0	65·8	0·21	2·6	0·02	210	3·5	200	62	76	128	1·77	38
June 9 station 1	8·25 8·3	93	0·023	2·3	0·05	270	0·26	45	8	88	120	1·42	44
June 9 station 2	7·30 8·3	90·6	0·01	1·9	0·02	270	0·16	57	3	94	128	1·42	41
June 10 station 3	7·58 8·35	92·5	0·015	2·2	0·03	280	0·20	62	7 0	98	136	1·42	46
June 10 station 4	7·70 8·3	94·1	0·017	2·1	0·02	280	0·19	62	7 9	100	144	1·77	45
June 11 station 5	7·90 7·9	96·8	0·019	2·0	0·02	260	0·16	50	5 4	100	132	1·77	38
June 18 station 1	8·96 8·4	81 125	0·008	2·4 3·3	0·03	230	0·11 0·10	40	9 1	78 95	112 130	0·71	38

All data derived from preserved water samples, except where two numbers occur in the same square: top number is derived from lab analysis of preserved samples; bottom number is derived from samples analyzed immediately in the field.

LIFE CYCLES AND DISTRIBUTION

I attempted to work out the life cycles of six aquatic insects. Sufficient information was obtained for *Pteronarcys dorsata* (Say) (Plecoptera) and *Ephemera simulans* Walker (Ephemeroptera) to provide a good picture of their life cycles. In comparison, the information obtained for the odonate *Ophiogomphus colubrinus* Selys and the plecopterans *Isoperla transmarina* Newman and *Taeniopteryx nivalis* (Fitch) was limited and certainly less revealing; but there were sufficient data to describe generally the life cycles of these species. Data obtained for *Isogenoides colubrinus* Hagen (Plecoptera) proved inadequate, providing only a rough indication of the duration and intensity of emergence.

Initially I constructed and analyzed nymphal size-frequency distributions (number of nymphs in each size class per each week sampled, combining all stations) and constructed graphs of the number of adults emerging over time. This could be done for all species except *Isogenoides*, although emergence data were lacking for *Ephemera*. Subsequently I used other criteria including some or all of the following for each species: (1) mean length of all nymphs during each sampling period (combining all stations); (2) mean length of all nymphs at each station over time, using various combinations of lengths and time units plotted against developmental stage (relative maturity); and (3) summarization of total numbers collected at each station.

Pteronarcys dorsata

Life Cycle

The stonefly *Pteronarcys* was very abundant at the study sites and information on its life cycle is, therefore, the most comprehensive. Raw data were initially converted into size-frequency histograms using 2 mm size classes. These data were plotted against weekly sampling intervals, all stations combined. Although the nymphs were measured to the nearest 1 mm, the extensive size range of different size classes occurring in any given sample suggested 2 mm size classes as logical working units. This facilitated the graphing of information and did not invalidate subsequent analyses. Grouping together data from all stations per week for the purposes of graphing also facilitated analysis, since each station taken separately could not have provided sufficient numbers. But this did make it impossible to compare different environments along the river. Although local factors are not emphasized for any species, they will be considered in the context of the general discussion and in brief sections on species' habitat preferences. The grouping of samples was done for all species; but for *Pteronarcys*, it also proved useful to construct histograms for station 5 in addition to the histograms representing all stations combined. Most *Pteronarcys* nymphs were collected from station 5 and a comparison among the mean length graphs of both sets of histograms proved useful.

Figures 14, 15 and 16 show the patterns of nymphal development and emergence in 1972. Emerging adults were not collected in 1972, but field observations of the earliest adults seen flying in large

Figure 14. Size-frequency distribution of *Pteronarcys dorsata* nymphs for 1972 (all stations combined).

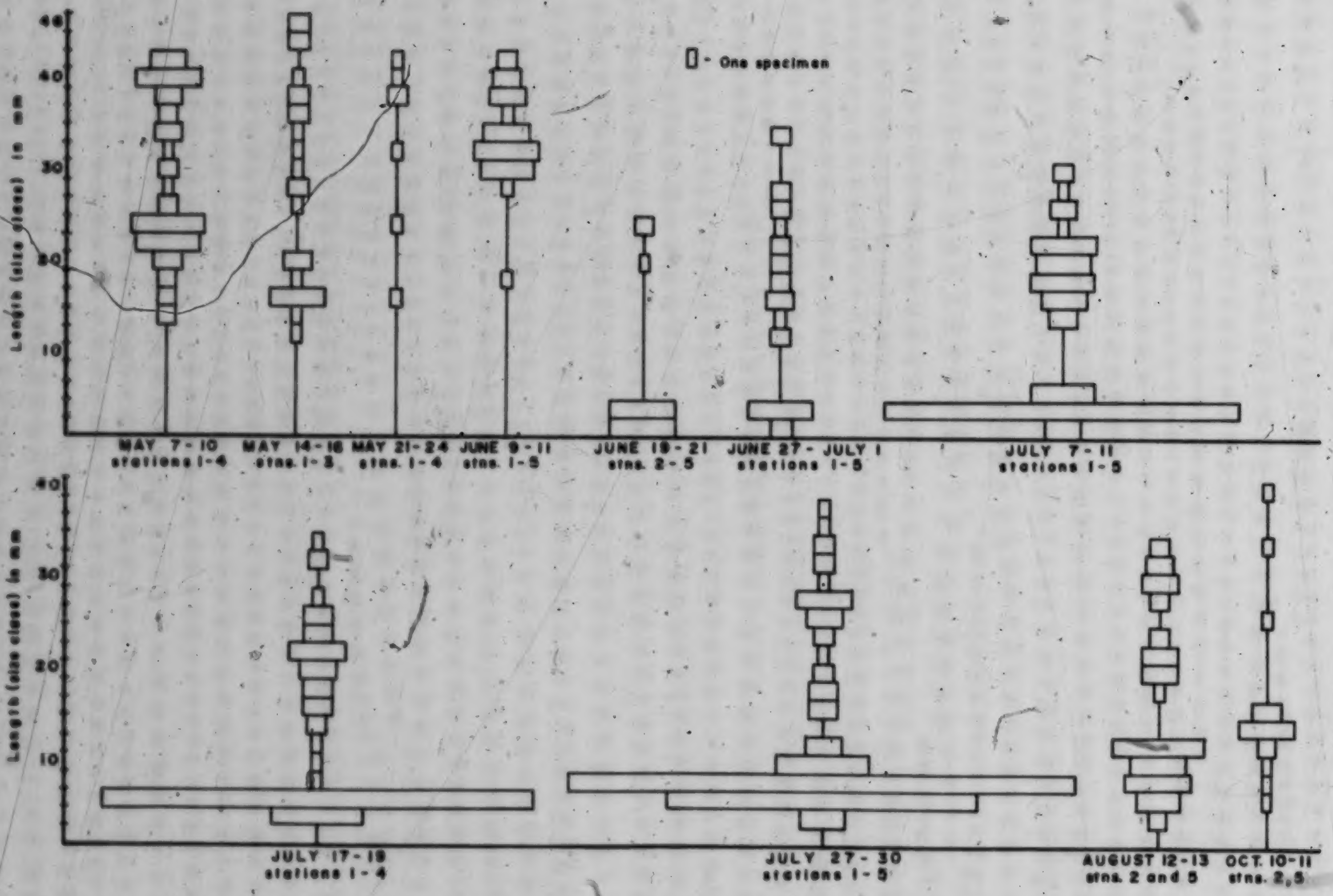

One specimen
Length (size class) in mm
10
20
30
40
MAY 7 - 10 stations 1-4
MAY 14-16 stns. 1-3
MAY 21-24 stns. 1-4
JUNE 9-11 stns. 1-5
JUNE 19-21 stns. 2-5
JUNE 27 - JULY 1 stations 1-5
JULY 7-11 stations 1-5
JULY 17-19 stations 1-4
JULY 27 - 30 stations 1-5
AUGUST 12-13 stns. 2 and 5
OCT. 10-11 stns. 2, 5

Figure 15. Size-frequency distributions of *Pteronarcys dorsata* nymphs for 1973 (all stations combined).

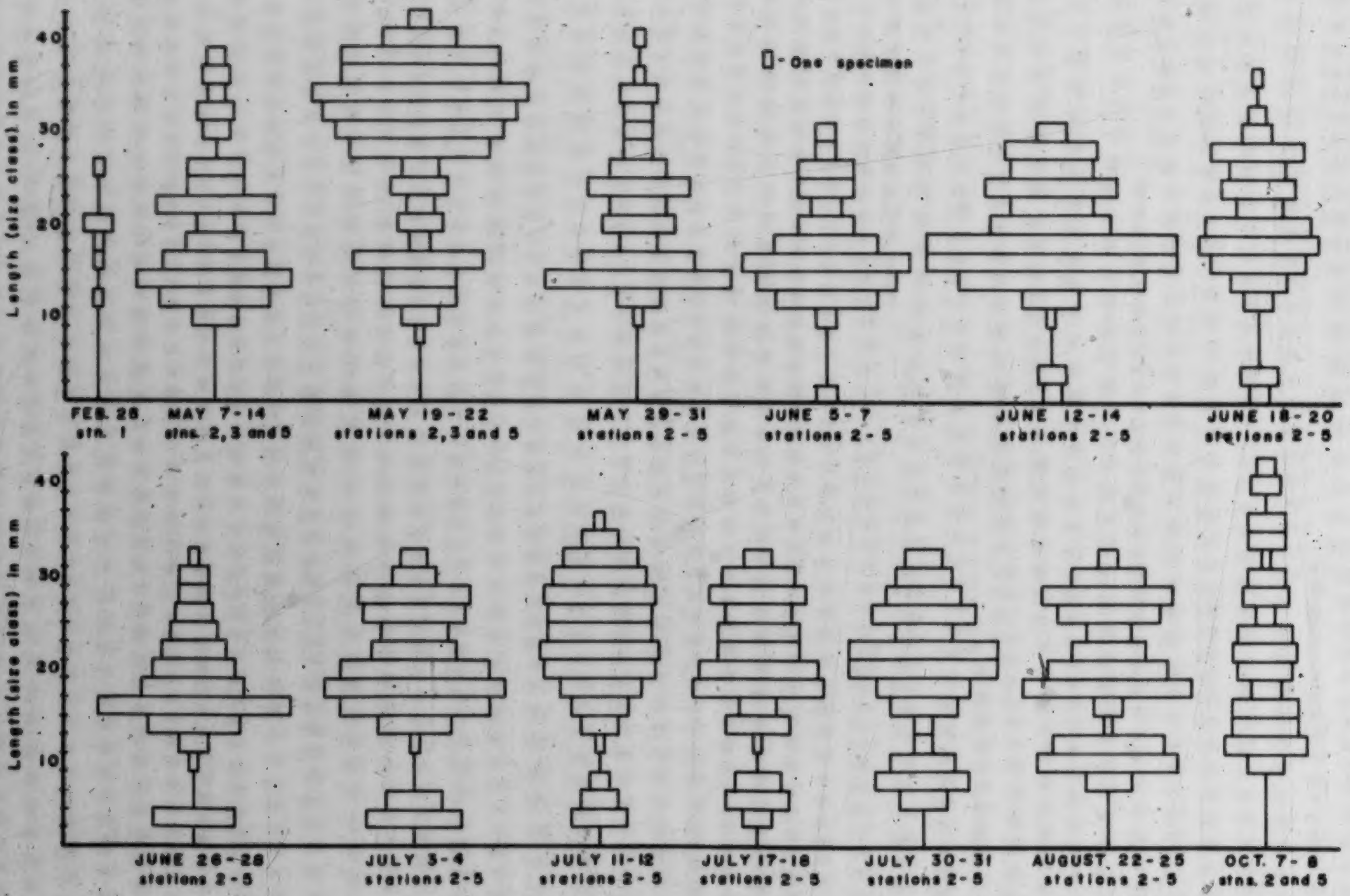
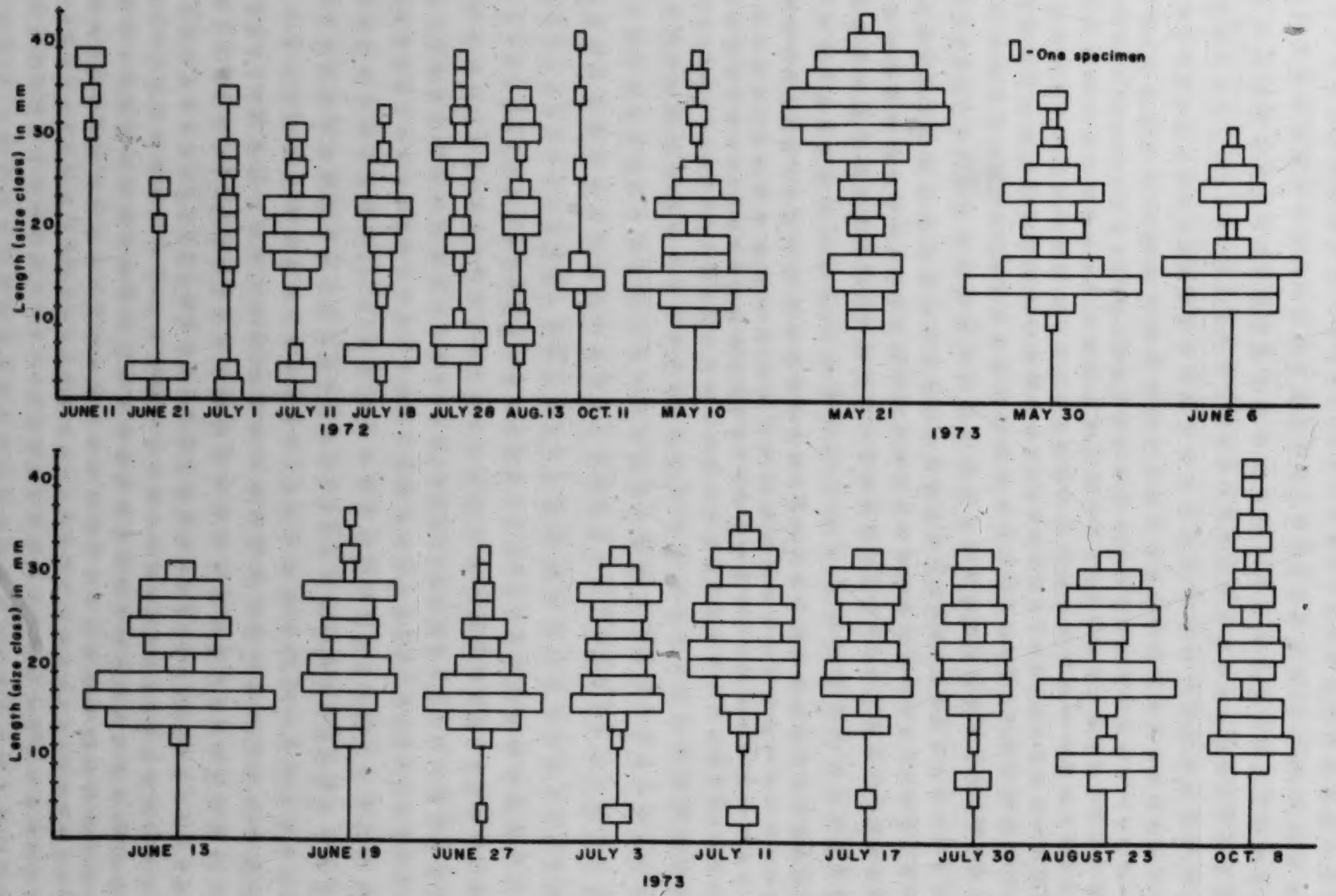

□ - One specimen
Length (size class) in mm
40
30
20
10
FEB. 28
stn. 1
MAY 7-14
stns. 2,3 and 5
MAY 19-22
stations 2,3 and 5
MAY 29-31
stations 2-5
JUNE 5-7
stations 2-5
JUNE 12-14
stations 2-5
JUNE 18-20
stations 2-5
Length (size class) in mm
40
30
20
10
JUNE 26-28
stations 2-5
JULY 3-4
stations 2-5
JULY 11-12
stations 2-5
JULY 17-18
stations 2-5
JULY 30-31
stations 2-5
AUGUST 22-25
stations 2-5
OCT. 7-8
stns. 2 and 5

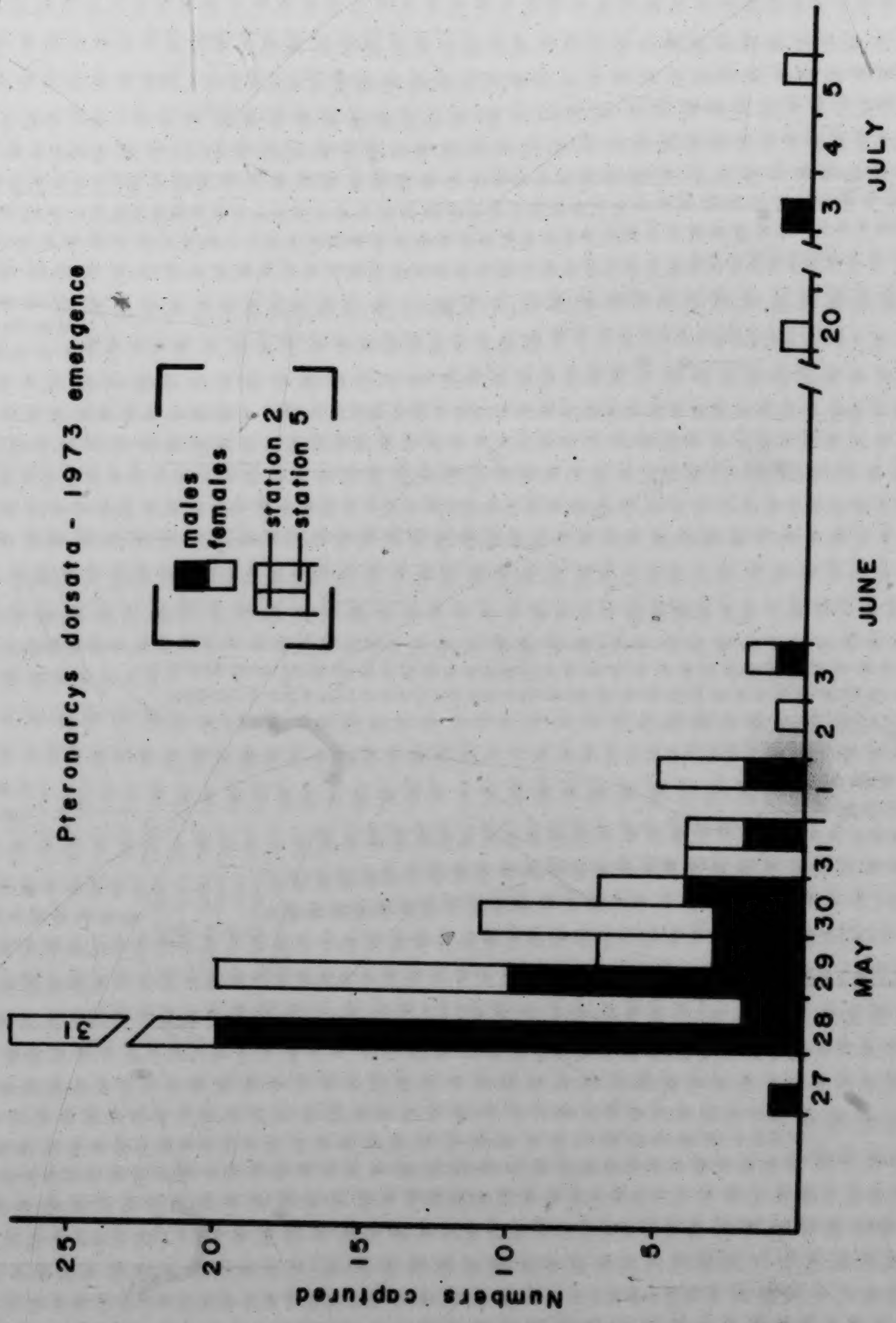
Figure 16. Size-frequency distributions of *Pteronarcys dorsata* nymphs for 1972 and 1973 (station 5).


□ - One specimen
Length (size class) in mm
10
20
30
40
JUNE 11
JUNE 21
JULY 1
JULY 11
JULY 18
JULY 28
AUG. 13
OCT. 11
1972
MAY 10
MAY 21
MAY 30
JUNE 6
1973
Length (size class) in mm
10
20
30
40
JUNE 13
JUNE 19
JUNE 27
JULY 3
JULY 11
JULY 17
JULY 30
AUGUST 23
OCT. 8
1973

numbers above the river shoreline were made in the evenings of June 21 and 22, 1972. This corresponded with the disappearance of the largest nymphs (28 - 38 mm, station 5; 26 - 42 mm, all stations) between June 9 and 21 and with the first appearance of very small nymphs (1 - 4 mm) in the June 19 - 21 samples. These very small nymphs probably represent nymphs hatching from eggs oviposited shortly after the suggested peak emergence. After this emergence period, two generally distinct groupings, or cohorts, of nymphs become obvious, one probably representing 1972's hatch and the other representing larger nymphs from the previous year. Each cohort generally remained distinguishable throughout 1972 and 1973, and both tended to increase in total length throughout the two-year period, increasing in numbers of larger size classes at the expense of the smaller size classes.

Data of Figures 14, 15, and 16, coupled with emergence data and general field observations, indicate a similar pattern of development in 1973. Data from emergence samples (Fig. 17) indicated that most of the nymphs emerged between May 27 and June 2, with field observations corroborating this. Many nymphs were seen congregating in shallow water near the shore on May 21, with the first adults emerging on May 27 and 28. Following emergence, many adults were seen flying over the river in the late evening, some as late as July 18. The size-frequency histograms show the largest nymphs (26 - 42 mm) disappearing from the samples between May 19 and 31, and very small nymphs appearing in June. As for 1972, after emergence, two cohorts could be distinguished: a cohort of large nymphs that probably hatched in 1972 and a cohort of small nymphs hatching in 1973. Mean length data help to substantiate

Figure 17. *Pteronarcys dorsata* emergence 1973.



Pteronarcys dorsata - 1973 emergence

the patterns indicated by the histograms. Figure 18 (mean length of all specimens from the weekly totals) shows a general increase in nymphal size until emergence starts.

An attempt was made to separate nymphs, via mean lengths, into cohorts that would indicate year of hatching and emergence (Fig. 19). The 1970 cohort includes mature nymphs generally longer than 28 mm and probably ready to emerge in June. These nymphs probably represent the 1970 hatch.

The 1971 cohort includes immature nymphs 12 - 30 mm in length probably representing the 1971 hatch. These immature nymphs grew during the summer after the 1972 emergence and into May, 1973, as indicated by the increase in mean lengths of nymphs over time. These are nymphs that emerged in late May and early June, 1973. Also the means from station 5 were much larger than those from any of the other stations during July and August, 1972, because the largest specimens were collected at station 5, the smallest at the other stations.

The 1972 cohort hatched in 1972. The loss of the largest nymphs (>26 mm) from the samples as a result of the late May - early June, 1973, emergence is indicated. There are two groups within this cohort. One group represents immature nymphs of unknown gender between 10 and 20 mm; the other group represents mostly immature male and female nymphs between 20 and 35 mm. The groups appear as separate cohorts, but if gender was not a factor in the determination of mean lengths, only one homogenous group would appear on the graph — a single cohort encompassing nymphs between 14 and 27 mm. I also separated the nymphs into males, females, and specimens of indeterminate gender to establish

Figure 18. *Ephemera*, *Isoperla*, and *Pteronarcys*: mean lengths of nymphs from all stations combined, from each sampling week.

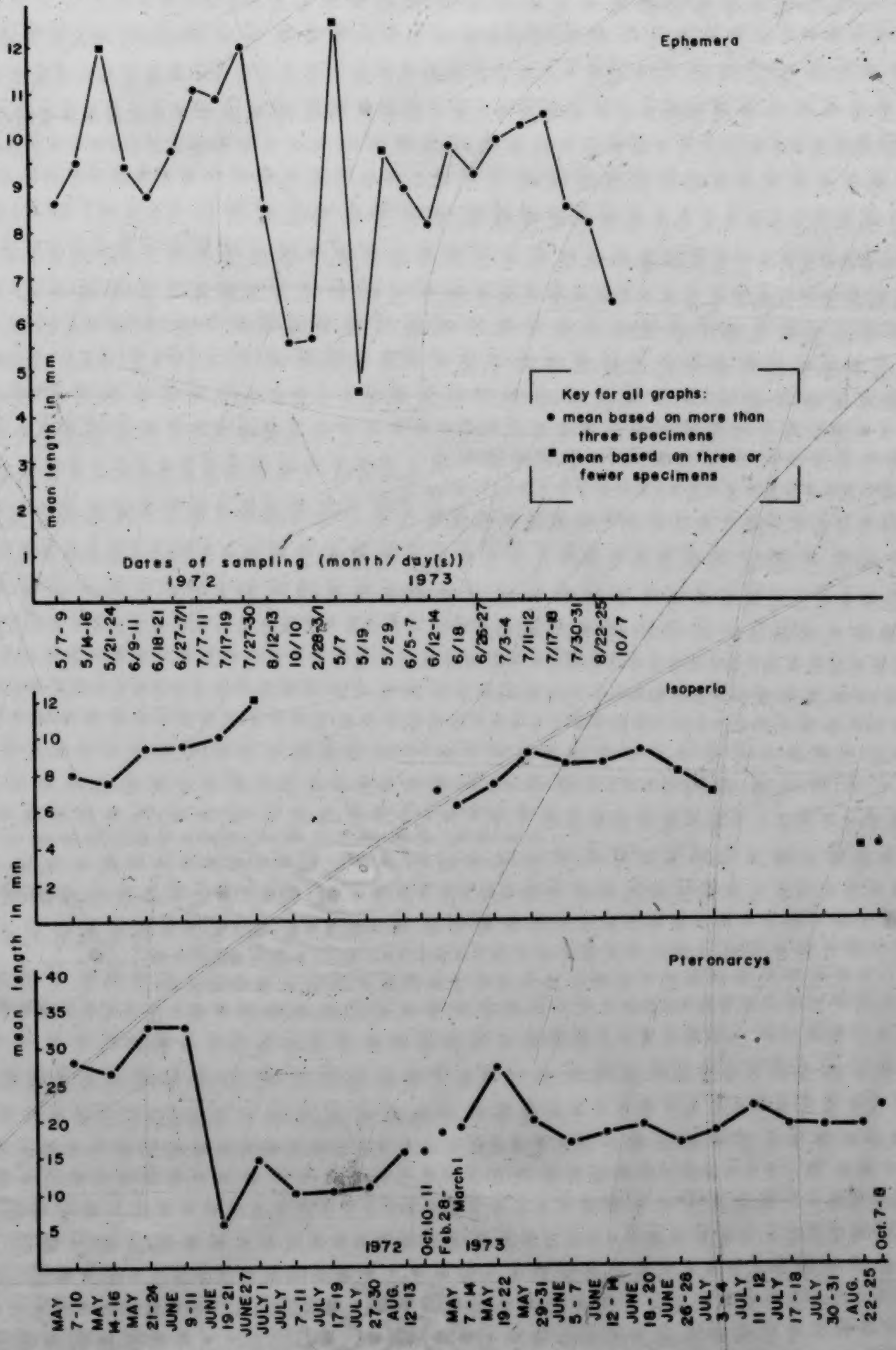
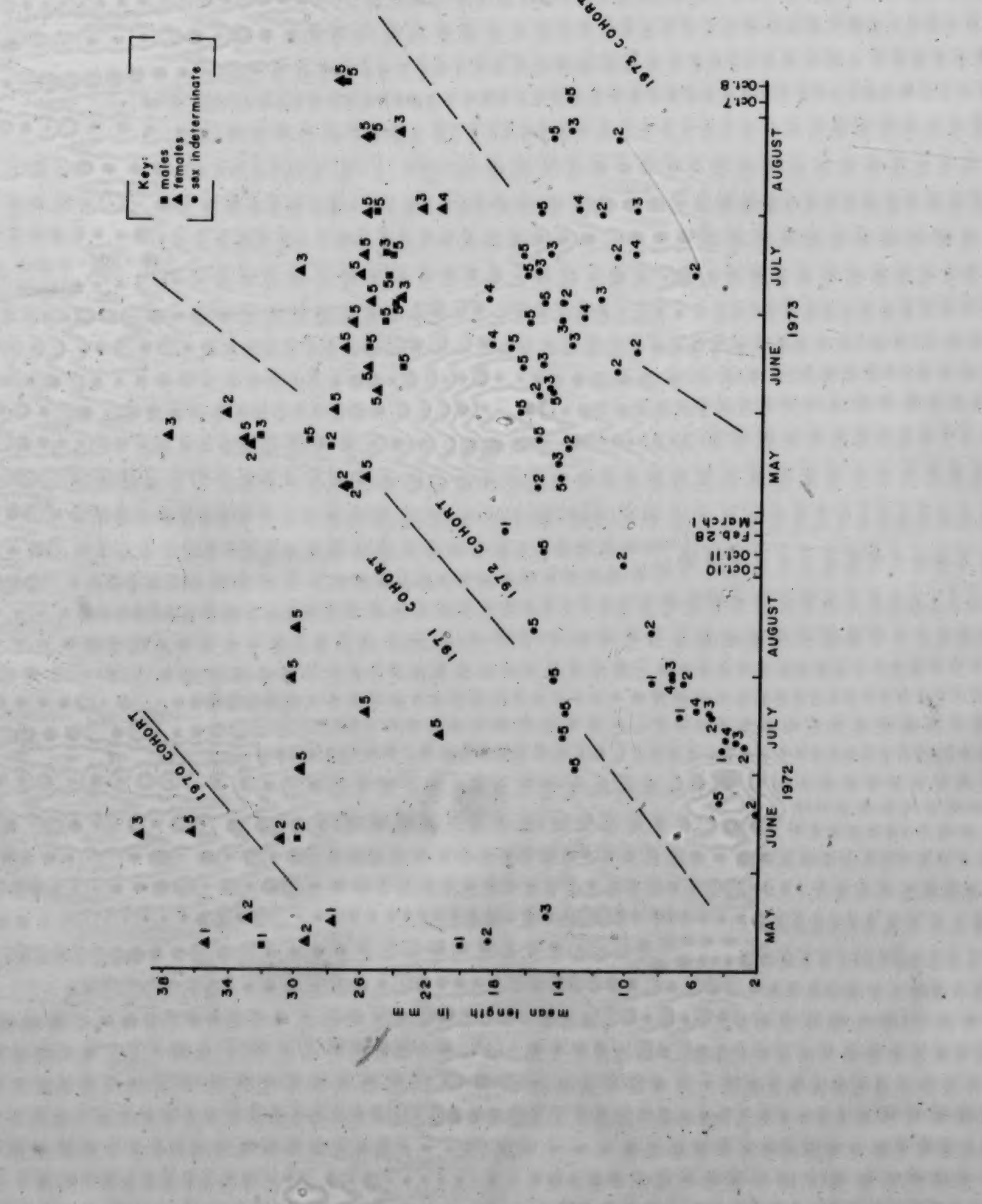

Ephemera
mean length in mm
1
2
3
4
5
6
7
8
9
10
11
12
Key for all graphs:
● mean based on more than three specimens
■ mean based on three or fewer specimens
Dates of sampling (month/day(s))
1972
1973
5/7-9
5/14-16
5/21-24
6/9-11
6/18-21
6/27-7/1
7/7-11
7/17-19
7/27-30
8/12-13
10/10
2/28-3/1
5/7
5/19
5/29
6/5-7
6/12-14
6/18
6/26-27
7/3-4
7/11-12
7/17-18
7/30-31
8/22-25
10/7
Isoperla
mean length in mm
2
4
6
8
10
12
Pteronarcys
5
10
15
20
25
30
35
40
1972
1973
MAY 7-10
MAY 14-16
MAY 21-24
JUNE 9-11
JUNE 19-21
JUNE27 JULY1
JULY 7-11
JULY 17-19
JULY 27-30
AUG. 12-13
Oct.10-11
Feb.28-March1
MAY 7-14
MAY 19-22
MAY 29-31
JUNE 5-7
JUNE 12-14
JUNE 18-20
JUNE 26-28
JULY 3-4
JULY 11-12
JULY 17-18
JULY 30-31
AUG. 22-25
Oct.7-8

Figure 19. *Pteronarcys dorsata*: mean lengths of male and female nymphs and nymphs of undetermined gender from each station, from each sampling run. Each number represents station of origin. Each cohort represents probable year of hatching. The dashed lines roughly separate the cohorts.


Key:
■ males
▲ females
● sex indeterminate
mean length in mm
36
34
30
26
22
18
14
10
6
2
MAY
JUNE
JULY
AUGUST
1972
Oct.10
Oct.11
Feb.28
March 1
MAY
JUNE
JULY
AUGUST
1973
Oct.7
Oct.8
1970 COHORT
1971 COHORT
1972 COHORT
1973 COHORT

a correlation between total length and relative maturity. Using these criteria, three categories can be recognized: (1) 1 - 10 mm nymphs, hatching in 1972 and growing that summer; (2) 10 - 20 mm nymphs, including a large proportion from the 1972 hatch and growing in 1973, and a smaller proportion possibly consisting of larger but still young to immature nymphs whose gender could not be ascertained; and (3) 20 - 30 mm nymphs, mostly large but immature nymphs whose gender could be determined; these were from the 1972 hatch and grew throughout 1973. Possibly there was also a small proportion of relatively small but mature nymphs emerging somewhat later than the peak of the 1973 emergence (late May - early June).

The 1973 cohort includes nymphs hatching in 1973 and probably emerging in 1975. The approximate time of hatching must be extrapolated from the growth trend and the time of emergence, since the means were derived from the much greater proportion of larger nymphs than from the early instars. This masking of early instars in 1973 is indicative of the general difference in content of 1973 samples as compared to 1972 samples: the 1973 samples contained a greater proportion of relatively large nymphs while the 1972 samples contained a greater proportion of small, presumably earlier instar nymphs.

Adults

The adult pteronarcids were probably nocturnal, at least with respect to flight behavior in this northern region. Many were seen flying at midnight above the river and even several meters from the river area above roadways. They are extremely clumsy fliers, which, along with their size, must make them susceptible to birds of prey.

Unfortunately, no pteronarcids were visually observed either emerging or ovipositing. Assuming that emergence was limited to no more than 2 weeks in late spring of both years, some information on longevity can be gleaned from field observations. Many of the adults must live as long as a month to 6 weeks, since some were seen in flight on June 12, 18, and 26, July 2 and 18, 1973. Emergence samples may support this if the specimens collected on June 20, July 3 and 5 had emerged earlier and merely crawled into the traps instead of having emerged in the traps (see Fig. 17).

Assumptions

The validity of *P. dorsata*'s life cycle pattern derived from my empirical data is based on certain assumptions which follow. Assumption 2 is particularly important for this species because it alludes to the difficulties inherent in the interpretation of life cycle data where overlapping generations are evident. The simultaneous presence of two or more generations in species taking more than 1 year to complete their life cycles complicates size-frequency distributions, especially when growth rate information and winter samples are unavailable. This clearly applies to *Ophiogomphus* and *Ephemera* as well and cannot be over-emphasized.

1) The total length of a nymph is directly proportional to its developmental stage; i.e. the larger the nymph, the greater its relative maturity. One criterion of relative maturity is the shape and development of the meso- and metathoracic wing pads (Table III and Fig. 20). Although there is considerable overlap between any two adjacent categories, one can predict into which category a nymph of any length should

Table III: Numbers and size classes of *Pteronarcys dorsata* nymphs in each maturity designation. (A "mature nymph" is one that is in the last nymphal instar and ready to emerge.)

Pteronarcys dorsata

Length (size class) in mm	M	I-M	I	Y-I	Y	VY-Y	VY	ND
50								
49								
48								
47								
46	1							
45	1							
44	3							
43	1							
42	4							
41	7							
40	14		1					
39	9							
38	13	1						
37	15							
36	15		1					
35	15		2					
34	16		4					
33	27		4					
32	21		13					
31	19		15					
30	19		25					
29	14		32					
28	13		49					
27	7		50					
26	2		41					
25	4		63		1			
24			59	1				
23			61	2	1			
22			49	6	2			
21			58	12	6			
20			44	27	14			
19			37	28	8			
18			28	37	27			
17			13	33	31			
16			6	39	39			
15			6	11	78			
14			2	11	57			
13				4	63			1
12				1	42	2		
11				1	39	6	4	
10					25	2	4	1
9					14	7	5	
8					9	11	19	1
7					4	4	36	2
6					1		22	18
5					1		24	33
4							33	23
3							34	17
2							12	4
1								

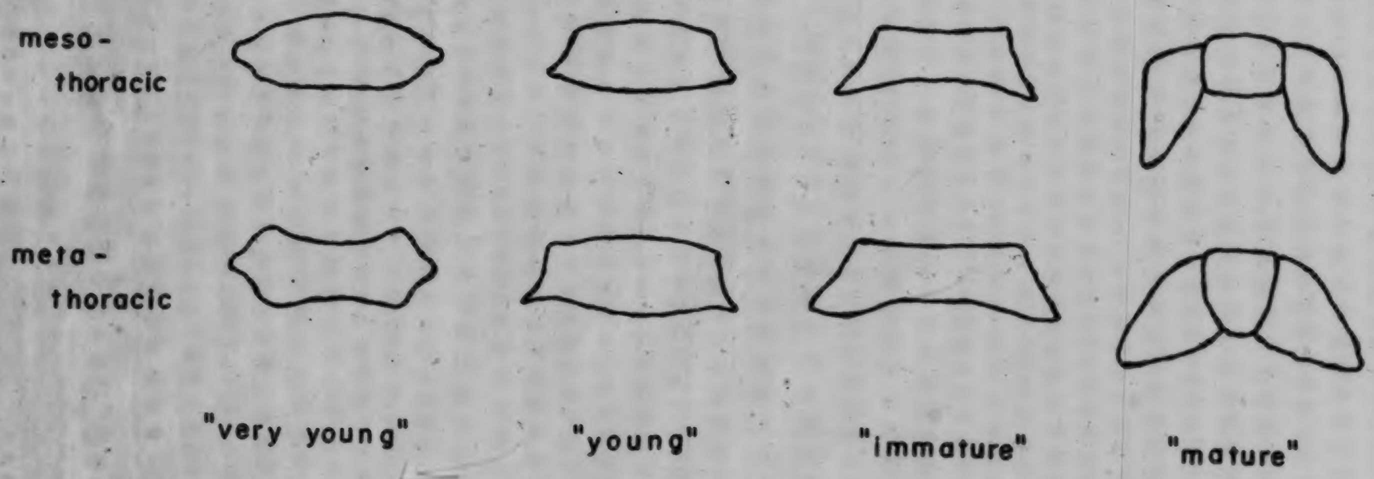
Key: for relative maturity based on wing pad condition -

M - mature; nymphs ready to emerge
I - immature
Y- young
VY- very young
ND- no maturity designation; wing pads very small or not visible

Other categories (I-M, Y-I, VY-Y) represent intermediate designations or indicate situations where nymphs could not easily be placed into one specific maturity designation or another

Figure 20: Wing pads of the nymph of *Pteronarcys dorsata* at four arbitrary stages of development.

Figure 20: wing pads of the nymph of *Pteronarcys* *dorsata* at four arbitrary stages of development


meso-
thoracic
meta-
thoracic
"very young"
"young"
"immature"
"mature"

(drawings not to scale)

be placed. For example, most nymphs 32 mm in length or longer will most likely be "mature." As size classes become smaller, predictability becomes more difficult because of the increasing overlap between categories and the difficulties inherent in distinguishing morphological features of wing pads. Although the categories are not definitive, the essential point is that there is a relationship between total length and relative maturity for the largest nymphs, an important factor in assessing a nymph's readiness to emerge.

2) The pteronarcids collected from the study area represent a localized, self-sustaining population, and the nymphs are members of contiguous yet overlapping generations. This statement could be construed as a tentative and general conclusion about *Pteronarcys dorsata* in the Kakisa River; but several other related assumptions, not proven themselves, relegate it to the status of an untested hypothesis. The first half of the statement is true, since no other closely related species have been found to cohabit the study area, and the study area itself is a geographically isolated environment with respect to *Pteronarcys*. The second half of the statement more closely conforms to a tentative conclusion, based on several size classes of nymphs (ranging between 2 and 46 mm) coexisting simultaneously within the study area.

3) Growth rates for individuals within any generation show predictable fluctuations within limits and generally conform to characteristic patterns of the entire generation. Conversely, patterns of growth for an individual within any generation are consistent with the overall patterns of the generation during its life cycle. For example, a nymph hatching in June of one year may grow slowly and steadily over the

autumn and winter, and then grow rapidly in early spring with a late spring emergence. All nymphs within that generation will conform to these patterns, with predictable but limited deviations dependent upon changes in some environmental conditions. One must also assume that nymphs from different stations within the study area do not demonstrate widely disparate patterns of growth and development; that is, the study area itself is 'an environment' *per se* with localized environmental conditions causing insignificant deviations from the general patterns.

The possibility of an egg-diapause or nymphal diapause or both cannot be determined from the material presented here. An extended egg-diapause, such as the 10 - 11 month egg-diapause of *Pteronarcys proteus* (Holdsworth, 1941), would extend the life cycle by that many months and might not show up in the histograms or other graphs.

4) No other lotic environment, except perhaps a stretch of Kakisa River immediately downstream of the study area, could contribute nymphs to the population established in the study area. The nearest river area large enough to contain other pteronarcid populations is that portion of Kakisa River upstream of the lake and about 11 km distant (it is often referred to as Tathlina River). This most certainly contributes no pteronarcids to the study area because of the intervening lake.

5) There are obvious differences in numbers of nymphs collected at any station during different sampling runs, between stations, between size classes, and even between years of the study (Table IV). And drift, particularly catastrophic drift, must certainly be a factor

here.

Both catastrophic and behavioral drifts would influence changes in both the relative proportions of different size classes of nymphs and the total number of nymphs within the study area at any given time. But such drifts would not remove entire generations or even a number of size classes.

Mortality rates probably vary among the instars as a result of different susceptibilities to catastrophic drift, predation (during spawning runs of grayling in particular), and other adverse environmental factors. Vulnerability is probably related to size, the amount of energy required for growth (and perhaps not available for other purposes), molting, other physiological factors, and factors associated with overall adaptability. But I do not believe any of these factors would so decimate any size class as to invalidate the assumption that the population is composed of contiguous yet overlapping generations.

Habitat Preference

Table IV lists the numbers of *P. dorsata* nymphs (and other species studied) that were collected at each station each year. A rough indication of preferred habitat can be inferred from these data simply by comparing total number of nymphs per station, the station having the greatest number of nymphs being the station with the preferred habitat. Obviously many factors, such as sampling procedures, will have been responsible for the differences in numbers between stations and even between the two years. Nevertheless, within limits, the numbers per station should be a rough indication of habitat preference. *Pteronarcys dorsata* would therefore seem to prefer the habitat of

Table IV: Numbers of specimens collected (4 species) at each station.

Table IV: Numbers of specimens collected (4 species) at each station

	PTERONARCYS					ISOPERLA					EPHEMERA					OPHIOGOMPHUS				
station	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
1972	60	150	80	41	187	68	104	71	38	2	134	150	28	22	20	2	9	11	12	55
1973	7	130	251	53	965	26	390	86	109	161	2	392	9	8	1	0	15	41	77	97
totals	67	280	331	94	1152	94	494	157	147	163	136	542	37	30	21	2	24	52	89	152

Discontinued sampling at station 1 in May, 1973

Sampling at station 5 began on June 11, 1972 station 5, especially in 1973. This station has the largest proportion of broken bedrock, rubble and riffles areas, the most turbulence, the least siltation and accumulation of either allochthonous or autochthonous material, and is the shallowest station. Station 4 appears to be the least preferred site, perhaps due to its location immediately below Lady Evelyn Falls where several factors may be significant. There are scouring and crushing effects of ice mounds that build up during the winter immediately below the falls and extending several meters downstream. There may be unknown disturbances related to frequent visits by tourists and local anglers at this station. Finally *P. dorsata* at station 4 might be preyed on heavily by fishes such as grayling, which must terminate their spawning run here.

Isoperla transmarina

Life Cycle

Information obtained on *I. transmarina* nymphs was inadequate for the accurate determination of this species' life cycle. Numbers collected varied widely, most of the specimens having been collected in May and early June of each year; and there was difficulty in confirming the identification of very small nymphs (very small nymphs were consequently excluded from data analysis). Therefore, neither distinct trends nor general patterns of growth and development could be clearly depicted. Nevertheless, there were substantial emergence data and these combined with some nymphal data suggest a definitive life cycle pattern. Information on adult behavior was totally lacking, so that verification of suggested periods of oviposition and hatching is impossible. The basis of the analysis was essentially the same as for *P. dorsata.* I used initially size-frequency distributions (plotting numbers in 1 mm size classes against consecutive weekly sampling periods where collections from all stations within each period were combined) and put much emphasis on emergence data.

There was an increase in the size of nymphs throughout May and June, 1972, and a decrease in the total numbers of nymphs collected through this period (Fig. 21). Nymphs continued to increase in size through June 28 (see Fig. 18). After this date, *I. transmarina* was absent from the samples. Emergence, therefore, probably took place in late May and June, although no emergence data were obtained to confirm this.

In 1973, there was also a general increase in the size and numbers of nymphs collected until the end of May, and thereafter a dramatic decrease in numbers and, to some extent, size (Fig. 21). There was a substantial loss of larger nymphs (8 - 12 mm) between May 31 and June 12, corresponding closely to emergence data, which show the bulk of emerging adults appearing between May 29 and June 13 (Fig. 22). The 1973 emergence data indicate that loss of nymphs was caused almost entirely by emergence. As was observed for *Pteronarcys*, large nymphs tended to congregate near the shore prior to emergence. When this phenomenon occurred, large numbers of nymphs could easily be collected.

As for 1972, early instars were poorly represented in the 1973 samples and very few nymphs of any size were collected after June. Nymphs of the new generation were probably present in the stream by August or September. If this was the case, then the presence of small

Figure 21. Size-frequency distributions of *Isoperla transmarina* nymphs for 1972 and 1973.

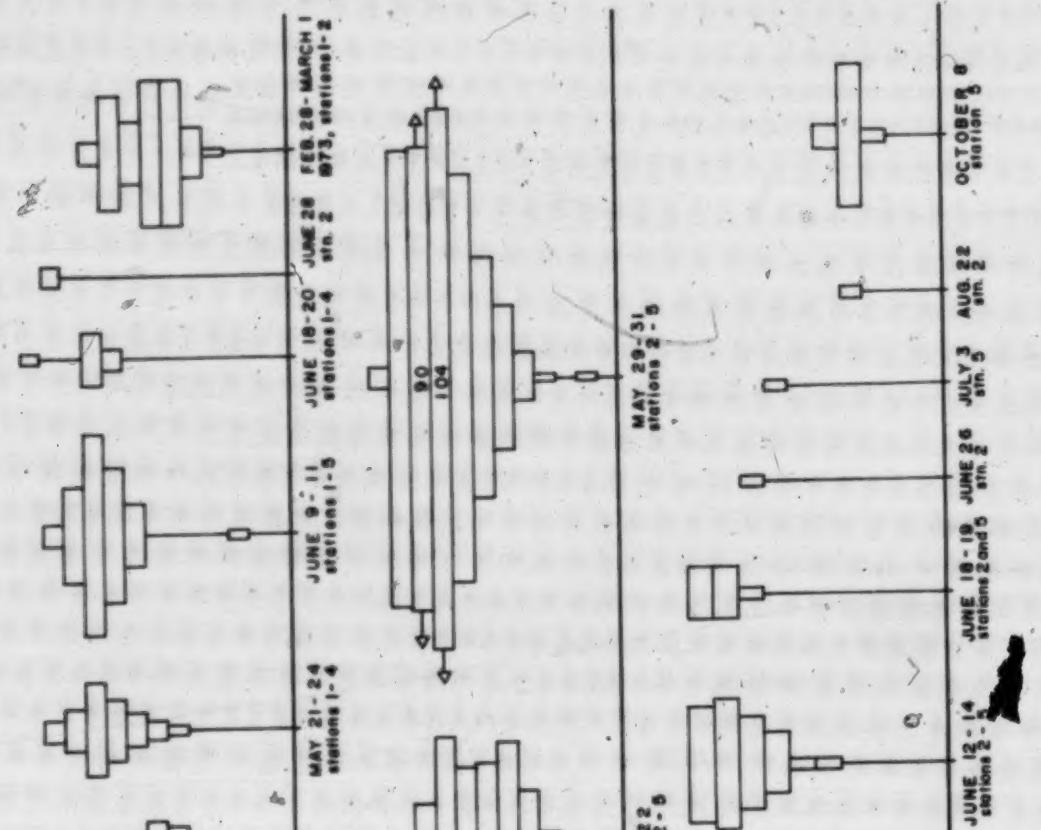
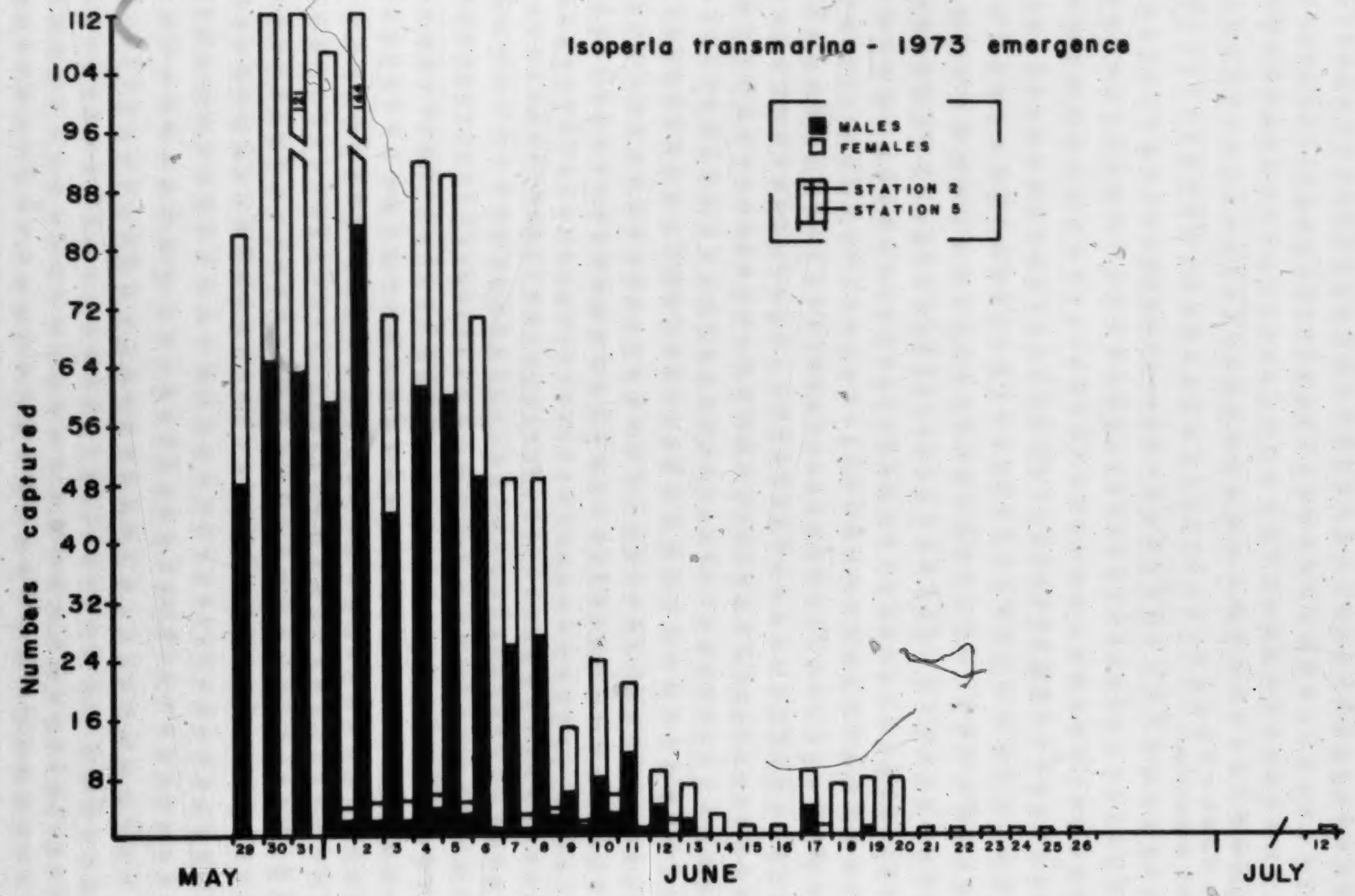

□ - One specimen
Length in mm
13
11
9
7
5
3
1
MAY 7-10, 1972 stations 1-4
MAY 14-16 stations 1-3
MAY 21-24 stations 1-4
JUNE 9-11 stations 1-5
JUNE 18-20 stations 1-4
JUNE 28 stn. 2
FEB. 28-MARCH 1 1973, stations 1-2
□ - One specimen
Length in mm
14
12
10
8
6
4
2
MAY 7-14, 1973 stations 2,3 and 5
MAY 19-22 stations 2-5
90
104
MAY 29-31 stations 2-5
□ - One specimen
Length in mm
11
9
7
5
3
1
JUNE 5-7, 1973 stations 2-5
JUNE 12-14 stations 2-5
JUNE 18-19 stations 2 and 5
JUNE 26 stn. 2
JULY 3 stn. 5
AUG. 22 stn. 2
OCTOBER 8 station 5

Figure 22. *Isoperla transmarina* emergence 1973.


Isoperla transmarina - 1973 emergence
MALES
FEMALES
STATION 2
STATION 5
Numbers captured
112
104
96
88
80
72
64
56
48
40
32
24
16
8
131
144
29
30
31
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
12
MAY
JUNE
JULY

nymphs in the February to May samples of both years may indicate some delayed hatching of eggs or even a general nymphal winter diapause or at least suspension of growth.

My data suggest that *I. transmarina* has a univoltine life cycle, and this supports Harper's (1973) field and experimental data for this species in southern Ontario. *Isoperla transmarina*'s life cycle in the Kakisa River generally conforms to the pattern described for it in Ontario: a fairly synchronous emergence period in May and June; oviposition in late May and June; an incubation period for the eggs lasting 30 - 40 days (depending on batch and incubation temperature); a hatching period commencing in August; rapid nymphal growth in the autumn and early winter until January; and then retarded growth until April. The severity of the boreal climate apparently causes each event in the life cycle to occur somewhat later in the Kakisa River than observed by Harper in Ontario.

Harper discovered some inexplicable peculiarities in the growth pattern in Ontario that caused some confusion. He noted a wide range of sizes in each of his samples and the occurrence of small (but not newly hatched) nymphs in his December sample, situations virtually duplicated in the Kakisa River. Harper suggested that incubation temperature could affect the extent of the incubation period and time of hatch. Harper also observed differences in nymphal development for stations with differing temperature regimes. Such conditions could perhaps explain the wide range of size classes collected from the Kakisa River during most of the sampling runs.

Assumptions

Most of the assumptions that apply to *Pteronarcys* can be applied to *I. transmarina*, with two general modifications:

1) Total length is assumed to be directly proportional to relative maturity, with the longest nymphs being the most mature. No other criteria for assessing maturity were used for *Isoperla*. Observations of wing pad shape and size were not made.

2) Most of the assumptions with respect to rate of growth of *Pteronarcys* can apply to *Isoperla*, with the exception of some differences related to the environmental conditions at each station and generalizations about diapause. The possible significance of an egg-diapause (or delayed hatch) and different temperature regimes among the stations is suggested.

Habitat Preference

Using the same assumptions as for *Pteronarcys*' habitat preference, station 2 would appear to be *I. transmarina*'s preferred habitat during 1972 and 1973 (see Table IV). This station is characterized by a substrate of medium-sized rocks and boulders, less angular than those found downstream, and is covered by a thin veneer of silt and organic detritus. *Potamogeton* sp. is also prevalent at this station, and the water is much less turbulent than it is downstream.

Ephemera simulans

Life Cycle

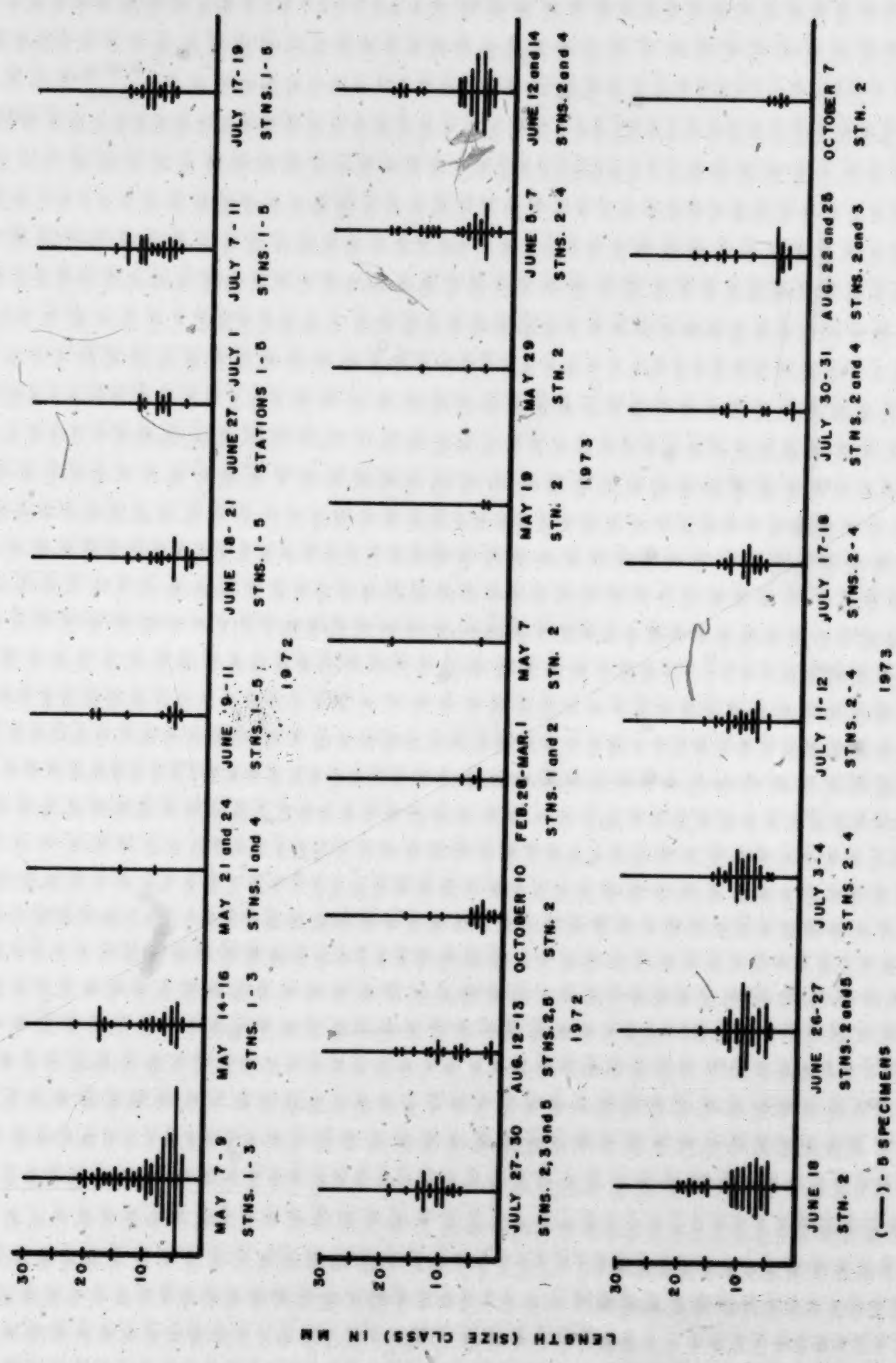
Sufficient nymphal data were gathered for *E. simulans* to determine its life cycle, even though information on emergence, oviposition, hatching, and seasonal rates of growth were lacking. Experimental rearing of nymphs in artificial environments would be necessary for a complete life cycle picture. Nevertheless, the various nymphal data provide relevant information.

Emergence probably occurred in late June, 1972, and mid to late June, 1973, based on the largest nymphs disappearing from the samples after these dates (Fig. 23). In both 1972 and 1973, eggs started to hatch probably in July, based on the appearance of very small nymphs in late July and August. The small nymphs present in the May, 1972 and 1973, samples would have hatched in 1971 and 1972, respectively. These small nymphs would indicate either delayed hatching or a drastic decrease in the rate of growth of these nymphs (perhaps even a nymphal diapause) over the winter.

There was a wide size range of nymphs in many of the samples from both years, most notably in early May, 1972 and during June, 1973 (Fig. 23). Average number of size classes per sample over both years was 8.6 with samples containing anywhere from 2 to 18 size classes. Average difference in size between the largest and smallest nymphs per sample was 11.7 mm with a range per sample of 1 to 18 mm inclusive. The presence of many size classes at any given time might indicate not only overlapping generations but such phenomena as delayed hatching, a poor relationship between total nymphal length and maturity, retarded growth or nymphal diapause, and a much more extensive emergence period than would be expected.

Figure 18 suggests an emergence period between late June and late July, 1972, and between mid June and mid July, 1973. During both years

Figure 23. Size-frequency distributions of *Ephemera simulans* nymphs for 1972 and 1973.


LENGTH (SIZE CLASS) IN MM
30
20
10
MAY 7-9 STNS. 1-3
MAY 14-16 STNS. 1-3
MAY 21 and 24 STNS. 1 and 4
JUNE 9-11 STNS. 1-5
1972
JUNE 18-21 STNS. 1-5
JUNE 27 - JULY 1 STATIONS 1-5
JULY 7-11 STNS. 1-5
JULY 17-19 STNS. 1-5
JULY 27-30 STNS. 2,3 and 5
AUG. 12-13 STNS. 2,5
1972
OCTOBER 10 STN. 2
FEB. 28-MAR. 1 STNS. 1 and 2
MAY 7 STN. 2
MAY 19 STN. 2
1973
MAY 29 STN. 2
JUNE 5-7 STNS. 2-4
JUNE 12 and 14 STNS. 2 and 4
JUNE 18 STN. 2
JUNE 26-27 STNS. 2 and 5
JULY 3-4 STNS. 2-4
JULY 11-12 STNS. 2-4
1973
JULY 17-18 STNS. 2-4
JULY 30-31 STNS. 2 and 4
AUG. 22 and 25 STNS. 2 and 3
OCTOBER 7 STN. 2
(—) - 5 SPECIMENS

the mean length increased substantially during the suggested emergence period, with dramatic decreases thereafter. Also, in 1973 nymphs with darkened wing pads (indicating the last nymphal instar) were present in the early June samples. These nymphs were obviously ready to emerge; and, although no *Pteronarcys-Isoperla*-type congregations in shallower water were noted, I assume that these large nymphs were relatively more accessible for collecting. They would therefore make up a large proportion in the samples during the emergence period, or at least during the beginning of the period. And this would account for the increased mean length of nymphs in the samples during June. Furthermore, many newly emerged adults were seen floating on the river surface on June 18 and 19 and swarming over the river during the late evenings of June 18, 19, 20, 26, and 27.

Hexagenia limbata, another large burrowing mayfly, is found in Kakisa Lake. It is conceivable that some of the adults I observed were in fact *Hexagenia*. However, there is no indication of the two species co-existing, *Hexagenia* remaining in the lake and *Ephemera* in the river (Lamoureux, 1973). Many dead mayflies, probably *Hexagenia* as well as *Ephemera*, were seen floating on the river on July 14 and 17 and on the lake July 16. So great were the numbers of dead mayflies that the shoreline, particularly around the dock at station 2, was choked with them, and there was a distinct odor of decomposition.

Information derived from averages is often difficult to interpret and often misleading, and herein lies the danger associated with making generalizations about such information as in Figure 18. These mean lengths were obtained from averages of all size classes of each species in each sample, regardless of gender, maturity criteria, or station of origin. Separate cohorts could be distinguished if the above factors were considered (Fig. 24 and Tables V and VI). These data are necessary for determining the life cycle of *Ephemera simulans*.

Figure 24 was constructed in a manner similar to Figure 19 (*Pteronarcys*) and can be analyzed in much the same way. The emergence period of *E. simulans* apparently occurred during the middle of May, 1972, and the middle of June, 1973, coinciding with the loss of the largest male and female nymphs from the samples. Nymphs probably representing the 1972 hatch were first noted in August; nymphs of the 1973 hatch were first noted in the latter part of July.

Cohorts based on probable year of hatching (and emergence) are shown in Figure 24. The 1970 cohort includes mature male and female nymphs that probably hatched in 1970 and emerged in 1972. The 1971 cohort includes nymphs of unknown gender (between mean lengths of 5 and 10 mm) that probably hatched in 1971 and would probably have emerged in 1973, larger male and female nymphs (between mean lengths of 11 and 14 mm) that could also have hatched in 1971 and probably emerged in 1973, and male and female nymphs (between mean lengths of 15 and 20 mm) that must have emerged in 1973 and probably hatched in 1971. Some of the intermediate sized nymphs (11 - 14 mm) may also represent part of a 1972 emergence, which extended into July, although very few nymphs larger than 15 mm were found after June, 1972 (Table V). Of all nymphs with darkened wing pads, only three were smaller than 15 mm (Table VI).

The 1972 cohort includes nymphs of indeterminate gender hatching

Figure 24. *Ephemera simulans*: mean lengths of male and female nymphs and nymphs of undetermined gender from each station, from each sampling run. Each number represents station of origin. Each cohort represents probable year of hatching. The dashed lines roughly separate the cohorts.

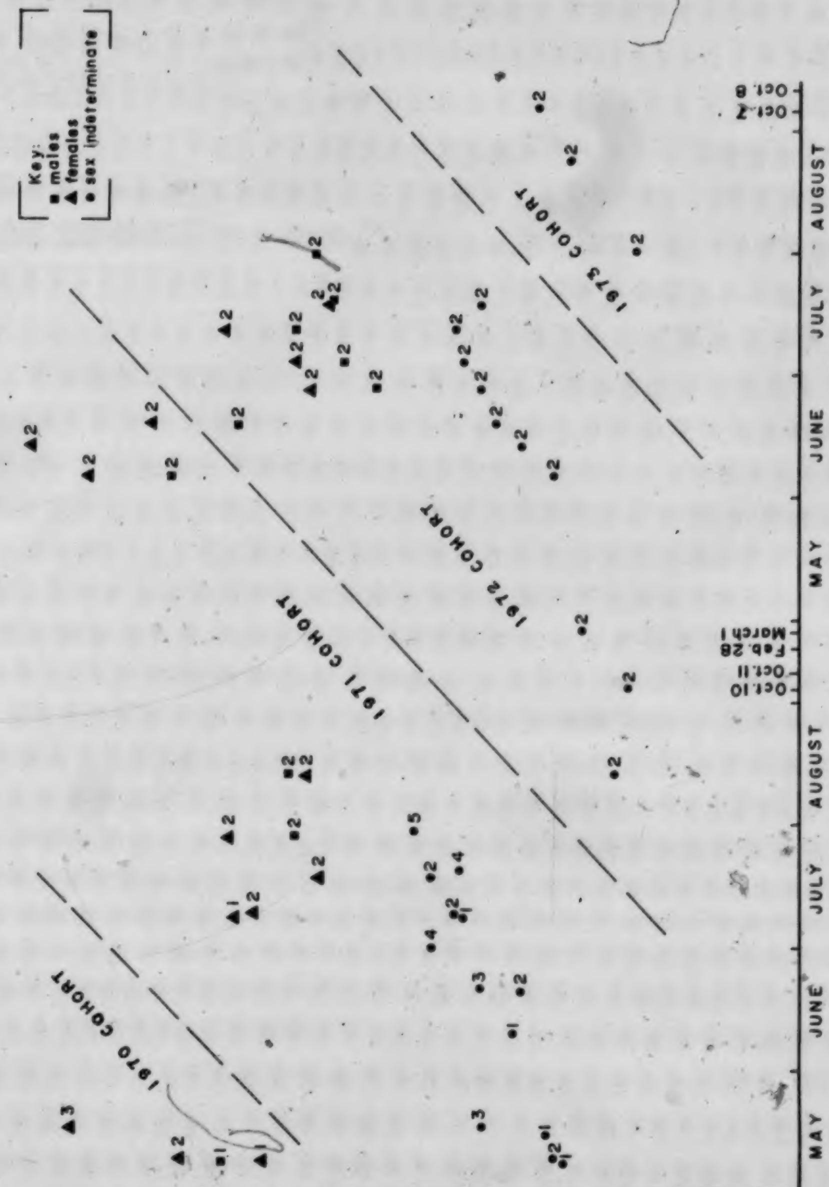

Key:
■ males
▲ females
● sex indeterminate
mean length in mm
18
16
14
12
10
8
6
4
2
MAY
JUNE
JULY
AUGUST
1972
Oct.10
Oct.11
Feb.28
March 1
MAY
JUNE
JULY
1973
AUGUST
Oct.7
Oct.8
1970 COHORT
1971 COHORT
1972 COHORT
1973 COHORT

Table V: Numbers of nymphs of *Ephemera simulans* in each size class and in each "maturity" designation per sampling week.

Key for relative maturity designations, based on wing pad coloration:

VD - very dark
D - darkened
P - partly darkened
U - not darkened
ND - no designation; wing pads very small or not visible.

		1972											1973													
		5/7-9	14-16	21-24	6/9-11	18-21	6/27-7/1	7-11	17-19	27-30	8/12-13	10/10	2/28-3/1	5/7	19	29	6/5-7	12-14	18	26-27	7/3-4	11-12	17-18	30-31	8/22-25	10/7
Condition of wing pads	VD																	4	6							
	D	2	2	1		2		1						1			6	2	1							
	P	11	2		1			1			2					1										
	U	31	8		3	7	6	25	23	29	13	3					7	1	16	30	24	13	19	6	8	
	ND	81	28	1	12	17	10	4	5		7	17	6	1	2	2	27	58	50	42	24	18	8	5	19	5
Length (size class) in mm	1																									
	2										4	2														
	3										2	2					1							3		
	4	9	2			3						6			1		1	5	1					1	4	
	5	31	9		2	4	1					4	4	1	1	1	10	8	9	3	1				5	1
	6	16	7		5			1			1	3	1				5	14	7	9	1	3			10	2
	7	14	4		3	8		3	2	1	3						6	13	10	8	4		2	1		1
	8	9	2		1	1	4	4	4	2	2		1			1	3	8	9	5	8	7	3	1		1
	9	6	2	1		2	3	3	3	1							2	5	7	13	8	4	3			
	10	7	2			1	4	2	2	5	1						1	5	7	16	6	3	7		1	
	11	5	1		1	2		2	6	5	4	1							7	4	9	4	5	2		
	12	3					1	5	6	2	1								2	7	5	2				
	13	4	1			1	3	5	2	7	1	1					2			5	2	4	4		2	
	14	2			1				1	3							2			1	3	1	2	2		
	15	4		1		3		5	2		1						2		3		1	2	1	1	2	
	16	2	1							1						1	2	1	2						1	
	17	2	2					1			1	1						1	2	1		1				
	18	5	6								1						1		3						1	
	19	1			2					2								2	2							
	20	3			1									1			1	2	2						1	
	21	2				1											1	1								
	22		1																							

Table VI: *Ephemera simulans* nymphs of any length (size class) in each "maturity" designation.

Ephemera simulans
Numbers of specimens collected in 1972 and 1973, showing the relationship between total length and relative maturity (based on condition of wing pads).

Length in mm	VD	D	P	U	ND
25					
24					
23					
22		1			
21	1	2	2		
20	3	3	2	3	
19	2		2	5	
18	2	4	4	7	
17	1	1	3	7	
16	1	3	1	6	
15		4	1	23	
14			1	17	
13			2	42	2
12				34	
11				54	4
10				40	30
9				15	48
8				12	64
7				6	77
6				1	84
5				1	94
4					33
3					8
2					6
1					

Key: for wing pad condition (relative maturity)

VD- very dark; nymphs ready to emerge
D- darkened
P- partly darkened
U- not darkened
ND- no maturity designation (wing pads very small or not visible)

in 1972 and probably emerging in 1974. Also included in this cohort are larger male and female nymphs that hatched in 1972. These would have emerged also in 1974. Possibly some of these large nymphs might have emerged in 1973, although no nymphs with darkened wing pads were found after mid June, 1973, and very few nymphs larger than 15 mm were collected after that time. The 1973 cohort includes nymphs that probably hatched in 1973 and would have been ready to emerge in 1975.

The wide range of mean nymphal lengths (6 - 14 mm) after the largest nymphs emerged indicates either large differences in the growth rates of nymphs or some kind of arrested state. Male and female nymphs found in July and August, 1972, and in late June and July, 1973, could be the result of nymphs growing rapidly from hatches in 1971 and 1972, respectively. Or the nymphs of indeterminate gender found throughout the summers of 1972 and 1973 could have resulted from either delayed hatching or egg diapause in 1971 and 1972, respectively, or arrested growth during the winters of 1971-1972 and 1972-1973, respectively. Another possibility is that the wide nymphal size range for immature nymphs found in both years could have come from the same group of nymphs found in May and June of each year, with some nymphs subsequently exhibiting a much more rapid rate of growth than others. If two generations contribute to these wide size ranges that existed after emergence and before hatching each year, this would indicate a life cycle of greater than 2 years for *E. simulans*.

Table V indicates the relative contribution each size class made to the sample and includes maturity criteria based on the darkened wing pads. Emergence apparently took place between May 7 and July 17, 1972, with a peak occurring in mid to late May and between May 7 and June 26, 1973, with a probable peak in mid to late June. These patterns are based on the presence and subsequent disappearance of large nymphs (about 16 - 22 mm) with partially darkened to very dark wing pads.

There were many small nymphs between 4 and 7 mm in most samples both years and especially in early to mid May, 1972, and June, 1973. This suggests several possibilities. Eggs oviposited in May of one year might have exhibited delayed hatching, resulting in small nymphs that grew slowly or not at all over the winter. Eggs oviposited in July of one year might not hatch until early spring the following year; or they might have hatched shortly after oviposition, with the small nymphs growing slowly or not at all during winter. Finally, eggs oviposited at any time might have resulted in nymphs growing only slowly until the next year, possibly going into nymphal diapause after hatching or during winter. A combination of delayed hatching and slow nymphal growth, with little or no growth in the winter, would seem to be the likeliest possibility, since emergence and therefore oviposition occurred mainly in late spring or early summer of both years.

Number of nymphs in successively larger size classes tends to increase at the expense of the smaller size classes over time. This indicates expected seasonal growth, at least from May through August each year, and this is supported by similar patterns indicated in Figure 24.

Utilizing Table V and Figure 24, one can predict the following developmental sequence for *E. simulans*:

1) The eggs hatch in late July and August. The small nymphs found

during this period must indicate each year's hatch.

2) The major growth period for nymphs ranging in size from about 4 to 14 mm takes place in May, June, and July. These were nymphs that had probably hatched in 1971 and 1972. These nymphs grow throughout the summer and attain sizes within the 8 - 20 mm range by the end of August.

3) There is a period of little or no growth starting in autumn and lasting for much, if not all, of winter. The presence of small nymphs (4 - 7 mm) in early spring of each year apparently is due to very little, if any, growth in winter.

4) Emergence apparently takes place in May and June, with some stragglers perhaps emerging as late as early July. Table VI indicates two cohorts of *E. simulans* nymphs based on wing pad features: a cohort of large maturing nymphs between 16 and 22 mm, having darkened wing pads in the categories P, D, and VD, and a cohort of smaller nymphs between 2 and 15 mm, having poorly developed wing pads. However, overlapping occurs between the two cohorts. For example, some large nymphs (19 - 20 mm) can have poorly developed wing pads, even during the emergence periods, and smaller nymphs (13 - 15 mm) can have relatively well-developed wing pads. This would point up the somewhat imprecise relationship between total length and developmental stage for mayflies in general (Clifford, 1970a, 1970b).

This discussion of the life cycle of *E. simulans* in the Kakisa River has dealt with various interpretations of the limited information available. Each organization of the data provides a somewhat different picture, particularly with respect to the duration of each life cycle stage and even the length of the entire life cycle. For example, a life cycle of 2 or 3 years was suggested, as was an emergence period of from 1 to 3 months (extending over May and probably June and possibly July). The confusion arising from these various interpretations, whether they were made from separate figures and tables or combinations of both, is related to the presence of overlapping generations, the imprecise relationship between nymphal length and developmental stage in this mayfly, and the paucity of data. I will nevertheless conclude that *E. simulans* has a 2 year life cycle in the Kakisa River.

Assumptions

Most of the assumptions that were made for stonefly life cycles also hold here. A major exception has to do with total length, which is not a good criterion for determining mayfly life cycles where there are overlapping generations, since linear measurements often do not correspond closely with developmental stage.

Habitat Preference

Table IV indicates a strong preference of *Ephemera* for the less turbulent environs of stations 1 and 2. This is in accord with the work of Cummins and Lauff (1969), who found that *Ephemera* nymphs generally favor gravel substrate. This type of substrate is prevalent at station 2. Apparently siltation, when it occurs to a limited extent over coarse substrates (such as at station 2), does not deter these burrowing nymphs. Cummins and Lauff suggest that the nature and abundance of detrital food materials would likely also be a factor in the distribution of *Ephemera* nymphs. Station 2 appears to have a more diverse and greater accumulation of detritus than the other stations.

Ophiogomphus colubrinus

Life Cycle

Size-frequency distributions for the odonate *Ophiogomphus colubrinus* are difficult to interpret because of the small numbers of nymphs collected and the wide range of size classes present in many of the samples (Figs. 25 and 26). Average number of size classes per sample for the entire study period was 9.7 with a range of 1 to 22. Average difference between the longest and shortest nymphs per sample was 18.6 mm. Neither the dragonfly's time of emergence nor time of hatching can be ascertained from Figures 25 and 26, because very large nymphs with well-developed wing pads and very small nymphs were found throughout the year during both 1972 and 1973. There is, however, a loss of large nymphs from the samples of July 1, 1972, and June 26 - 28, 1973, and this was shortly after I had visually observed emergence. The small nymphs in the late July 1972 samples might indicate the new generation.

In 1972 hatching apparently occurred some time in late July (Table VII). This is suggested by the initial occurrence of 3 mm nymphs in the July 27 - 30 samples; these nymphs would most likely not represent the previous year's hatch.

The emergence of *Ophiogomphus* was easy to monitor, even without emergence traps. No traps were used in 1972, field observations being sufficient to afford an accurate description of the entire emergence period. Similar observations were made in 1973 and I also used shore-type emergence traps in 1973. Emergence for this species is obviously well synchronized. During both years, emergence took place almost entirely within a 4 day period, with the large green adults emerging in such large

Figure 25. Size-frequency distributions of *Ophiogomphus colubrinus* nymphs for 1972.

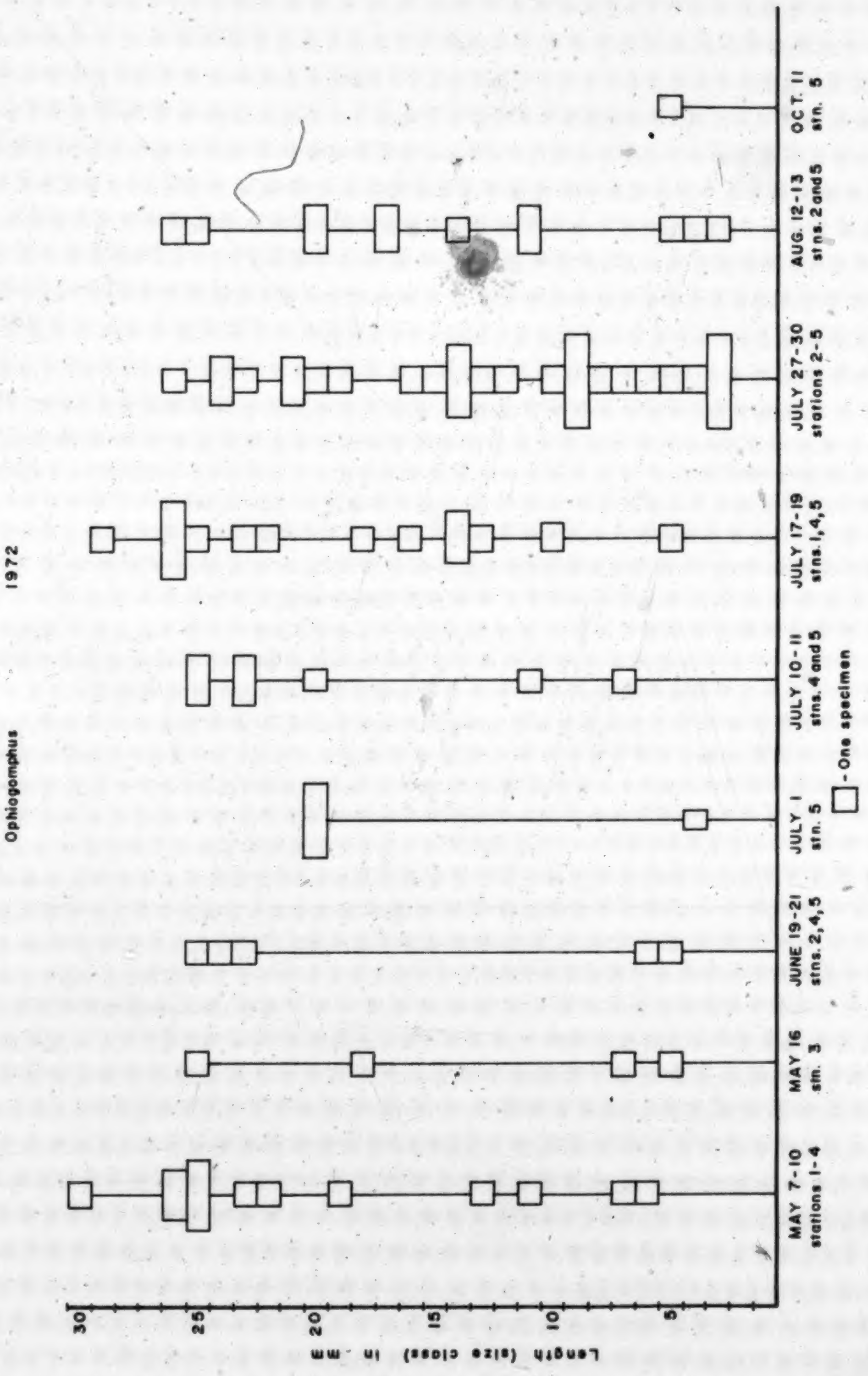

Ophiogomphus
1972
Length (size class) in mm
30
25
20
15
10
5
MAY 7-10
stations 1-4
MAY 16
stn. 3
JUNE 19-21
stns. 2,4,5
JULY 1
stn. 5
JULY 10-11
stns. 4 and 5
JULY 17-19
stns. 1,4,5
JULY 27-30
stations 2-5
AUG. 12-13
stns. 2 and 5
OCT. 11
stn. 5
□ - One specimen

Figure 26. Size-frequency distributions of *Ophiogomphus colubrinus* nymphs for 1973.

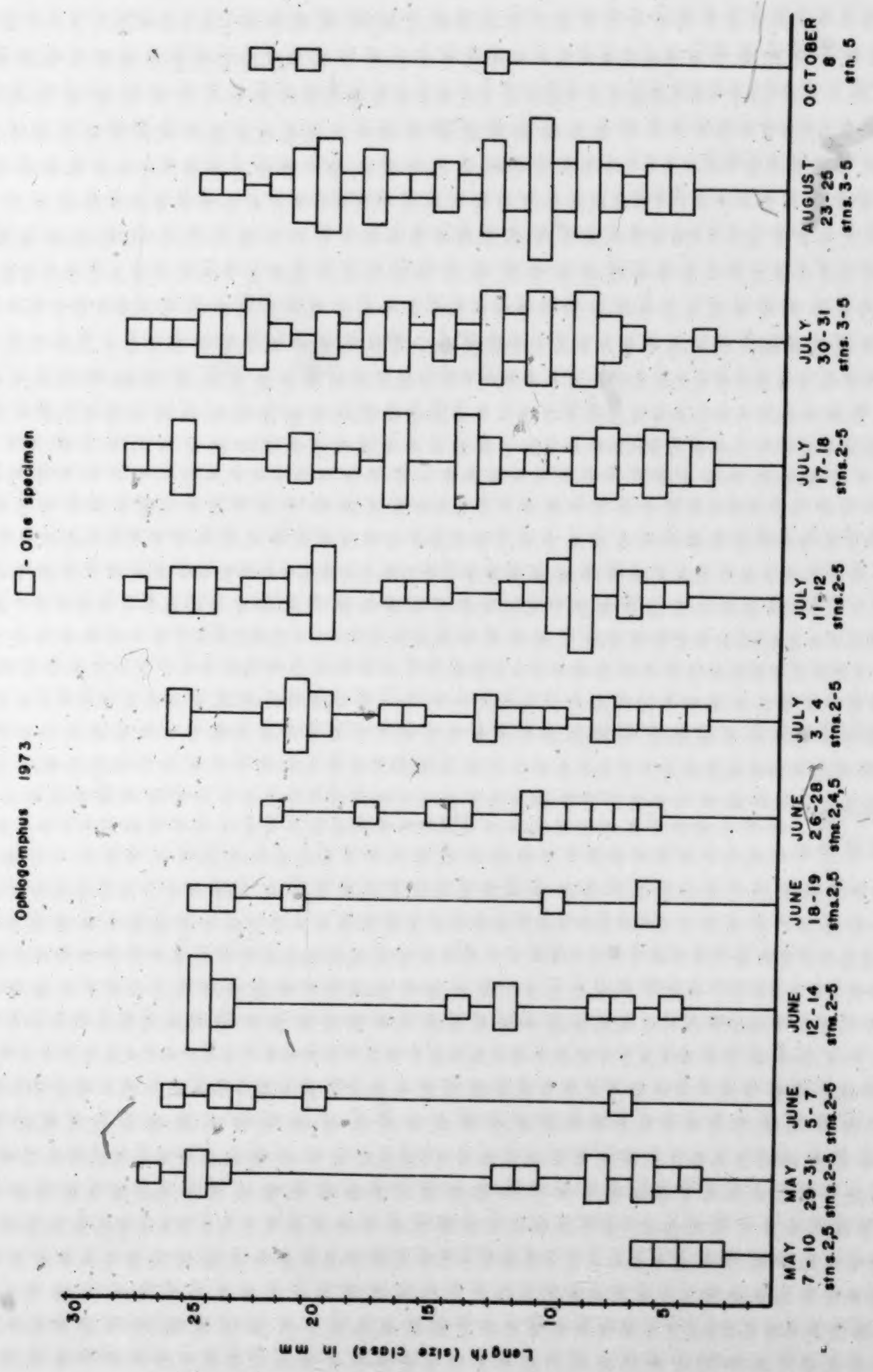

Ophiogomphus 1973
□ - One specimen
Length (size class) in mm
30
25
20
15
10
5
MAY 7-10 stns. 2,5
MAY 29-31 stns. 2-5
JUNE 5-7 stns. 2-5
JUNE 12-14 stns. 2-5
JUNE 18-19 stns. 2,5
JUNE 26-28 stns. 2,4,5
JULY 3-4 stns. 2-5
JULY 11-12 stns. 2-5
JULY 17-18 stns. 2-5
JULY 30-31 stns. 3-5
AUGUST 23-25 stns. 3-5
OCTOBER 8 stn. 5

Table VII: Number of specimens of *Ophiogomphus colubrinus* in each size class collected during each sampling week, providing relative maturity criteria based on lengths of meso- and metathoracic wing pads.

Key: x = number of specimens
t = length of metathoracic wing pads in mm
s = length of mesothoracic wing pads in mm

For example, 2-7-6 means x = 2, t = 7, s = 6
3°1°1 means x = 3, t < 1, s < 1

Single numbers mean that wing pads were too small to be measured.

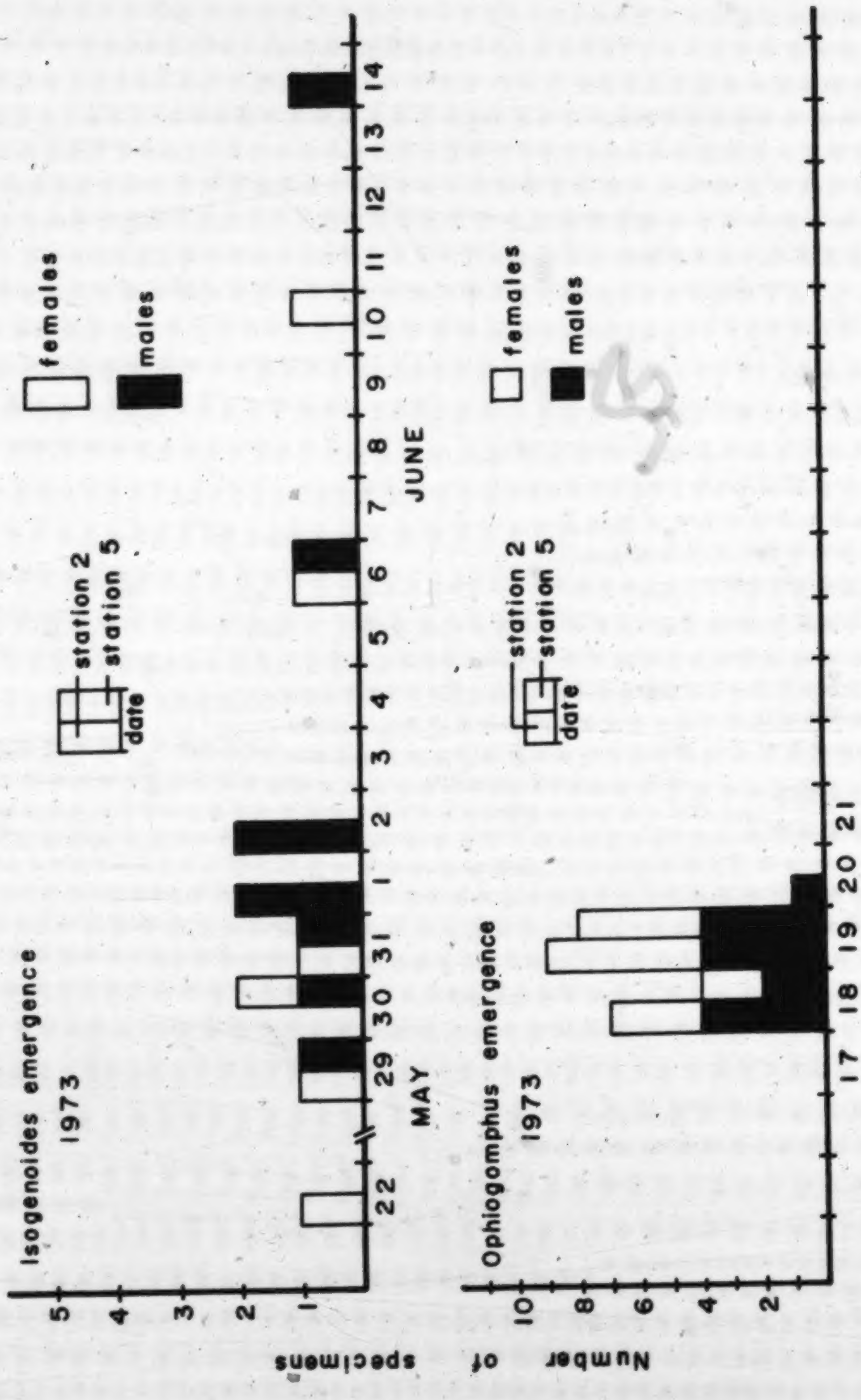
Key (on table): 3C = 1-6-7, 1-7-7, 1-3-3
(May 7 - 10, 1972, 25 mm)

Length (size class) in mm	1972 5/7-10	5/16	6/19-21	7/1	7/10-11	7/17-19	7/27-30	8/12-13	10/11	1973 5/7-10	5/29-31	6/5-7	6/12-14	6/18-19	6/26-28	7/3-4	7/11-12	7/17-18	7/30-31	8/23-25	10/8
30	1-7-7																				
29						1-7-7															
28																	1-7-7	1-7-7	1-7-7		
27											1-6-7							1-7-7	1-7-7		
26	1-7-7 1-6-7					3-7-7	1-7-7	1-7-7				1-7-7				2-7-7	1-7-7 1-6-6	3-7-7	1-7-7		
25	3-C	1-7-7	1-7-7		1-7-7 1-6-7	1-7-7		1-7-7			2-7-7		4-7-7	1-7-7			2-7-7	1-7-7	2-7-7	1-6-7	
24			1-7-7				2-7-7				1-6-6	1-7-7	2-7-7	1-7-7					2-7-7	1-6-6	
23	1-3-3		1-7-7		1-7-7 1-6-6	1-6-6	1-6-6					1-6-7					1-3-3		3-3-3		1-6-7
22	1-3-3					1-6-6									1-3-3	1-3-3	1-3-3	1-3-3	1-3-3	1-3-3	
21							2-3-3							1-3-3		3-3-3	1-6-6 1-3-3	2-3-3		3-3-3	1-3-3
20				[illegible]	1-3-3		1-3-3	2-3-3				1-3-3				1-6-6 1-3-3	4-3-3	1-3-3	2-3-3	4-3-3	
19	1-3-3						1-3-3											1-2-2	1-3-3	1-3-3	
18		1-3-3				1-2-2									1-2-2				1-3-3 1-2-2	2-3-3 1-1-1	
17								2-1-1								1-2-2	1-2-2	1-2-2 3-1-1	2-2-2 1-1-1	1-1-1	
16						1-2-2	1-1-1									1-1-1	1-1-1		1-2-2	1-2-2	
15							1-1-1								1-1-1		1-2-2		2-1-1	2-1-1	
14						1-1-1 1o1o1	3o1o1	1o1o1					1o1o1		1			1-1-1 3o1o1	1-1-1	1-2-2	
13	1o1o1					1o1o1	1o1o1									1-1-1 1o1o1		2o1o1	1-1-1 3o1o1	4-1-1	1-1-1
12							1				1o1o1		2o1o1			1o1o1	1-1-1	1o1o1	2o1o1	1-1-1 1o1o1	
11	1				1			2			1				2	1	1	1o1o1	3o1o1 1	2-1-1 4o1o1	
10						1	1o1o1							1o1o1	1	1	1o1o1 2	1	1o1o1 2	2o1o1	
9							4								1		5	2	1o1o1 3	1o1o1 3	
8							1				2		1		1	2		3	2	2	
7	1	1			1		1					1	1		1	1	2	2	1	1	
6	1		1				1			1	2			2	1	1	1	3		2	
5		1	1			1	1	1	1	1	1		1			1	1	2		2	
4				1			1	1		1	1					1		2	1		
3							4	1		1											
2																					
1																					
column totals	13	4	5	3	7	14	29	12	1	4	12	5	12	6	11	21	30	38	44	44	3

numbers as to literally cover riverbank vegetation. In 1972 most of the emergence took place on June 28 and 29. Individual nymphs were observed crawling from the water, drying for about an hour, going through the ultimate molt, and completing development for flight. The whole process from crawling out of the water to flight took about 2 hours. In 1973, many nymphs appeared ready to emerge on June 12, with emergence taking place from June 17 - 20 (Fig. 27). The largest numbers of emerging adults were observed on June 18. Although only two adults were seen *in-copula*, their occurrence in this state on July 11 suggests that oviposition occurred a few weeks after emergence.

I cannot make definite conclusions with respect to the length of the life cycle of this species because it was very difficult to interpret the available data. Not only were the numbers collected small but the presence of such a wide range of size classes in each sample further confused the picture, suggesting at least 2 overlapping generations and the possibility of a nymphal or egg diapause or at least arrested growth at some stage (Table VII). Corbet (1962) indicated that many temperate dragonflies have a diapause in the final larval instar. Such species are called "spring species" since they usually emerge synchronously, explosively (a substantial proportion of the annual population emerging on a single day from a single habitat), and early. Corbet also indicated that the final instar larvae of these spring species are habitually found in the summer (presumably after the annual emergence time) without signs of metamorphosis. Available data for *Ophiogomphus colubrinus* in the Kakisa River seem to conform to this pattern: emergence is early, synchronous, and explosive and many apparently well-developed larvae were

Figure 27. *Isogenoides colubrinus* and *Ophiogomphus colubrinus* emergence 1973.


Isogenoides emergence
1973
females
males
station 2
station 5
date
Number of specimens
5
4
3
2
1
22
29
30
31
1
2
3
4
5
6
7
8
9
10
11
12
13
14
MAY
JUNE
Ophiogomphus emergence
1973
10
8
6
4
2
17
18
19
20
21
JUNE

found in the samples well after emergence time (Fig. 27 and Table VII). This information, combined with Corbet's suggestion that a larval development period of 4 years is probably not uncommon for temperate gomphids, enables me to tentatively conclude that *Ophiogomphus colubrinus* takes at least 2 years to complete its life cycle in the Kakisa River.

Assumptions

Although wing pad length may be closely related to the total length of *O. colubrinus* nymphs, this criterion cannot be used for the exact determination of relative maturity, especially the readiness-to-emerge stage. More precise information on developmental stages is required for a complete life cycle study.

Information on growth rates is also required, including the monitoring of oviposition, hatching, diapause (if any), and possibly significant environmental factors. I assumed for all species that patterns of growth for individual nymphs within any generation conform to the overall pattern for that entire generation, with only minor individual variations.

Habitat Preference

Table IV indicates that *Ophiogomphus* probably prefers rocky, fast-flowing, turbulent and generally vegetation-free habitats. Nymphs were found most often at the stations below the waterfall, especially at station 5 in both years. The nymphs were usually found attached to the relatively flat undersurface of rock slabs and rubble in these areas. This is a microhabitat to which the nymphs seem morphologically suited, the nymphs being flattened dorsally and laterally, and having sharp tarsal claws on laterally extended legs.

Isogenoides colubrinus

Field observations provided some information on the emergence periods of other insects in the Kakisa River. And the emergence period of the stonefly *Isogenoides colubrinus* was determined in 1973 by using shore-type emergence traps.

Although the number of *I. colubrinus* adults was very low, Figure 27 indicates emergence in late May and early June, 1973. The specimens collected June 6, June 10, and June 14 might nevertheless have been attracted to the trap several days after they had in fact emerged.

Any conclusion with respect to the length of the life cycle of *I. colubrinus* would be entirely speculative because data are lacking. Yet it is possible that this species, as one of the larger stoneflies in the Kakisa River, would have a life cycle of 2 years. Since this species emerges in late May and probably grows very slowly during the long winter, it is logical to assume that it could not attain lengths of 20 - 25 mm (of the few late-instar nymphs that I found) in less than 2 years.

Taeniopteryx nivalis

Several species of *Taeniopteryx* are known to be winter species, growing during the colder months and emerging in early spring, and this probably holds true for *T. nivalis* in the Kakisa River. Only 17 nymphs were found during the study period, and these were taken in winter (Table VIII). Two female adults were found in early May; their occurrence corresponds with the end of ice conditions on the river in both years.

Table VIII. Number and size of *Taeniopteryx nivalis* nymphs collected in 1972 and 1973.

Table VIII: Number and size of Taeniopteryx nivalis nymphs collected in 1972 and 1973

Collection date	Station	Number collected	Length of nymphs (mm)
10 October 1972	2	3	5
		8	6
		1	7
11 October 1972	5	1	4
		1	6
28 February 1973	1	1	12
		1	15
1 March 1973	2	1	11
7-10 May 1973	2 adult females		

Although only 17 nymphs were found during the study period, I can tentatively conclude that *T. nivalis* has a univoltine life cycle in the Kakisa River. Also, it is clear that *T. nivalis* is a winter species with most of its growth occurring during the coldest months. The works of Coleman and Hynes (1970a) in southern Ontario, Harper and Hynes (1970) in eastern Canada generally, and especially Robertson (1967) in Alberta support these conclusions. Table VIII provides the available data on this species.

A provisional list of Plecoptera species from the Kakisa River is given in Appendix II. The stoneflies were identified from adult specimens by Dr. W.E. Ricker, Fisheries Research Board of Canada, Nanaimo, British Columbia.

DISCUSSION

Comprehensive faunistic studies of aquatic environments have been undertaken to only a limited extent in Canada's northland. Much of the area north of latitude 60° has come to the attention of the public only through discussion of natural gas pipelines and oil, and the possible sociological and general environmental impact of these activities. Hence, concern for the stability of the soil and tundra, the safety of migratory vertebrates, and the livelihood of native peoples has become paramount. But any consideration of the northern environment must transcend the immediately practical and even the long-term projections that superimpose man's activities upon such important ecosystems. Less obvious and seemingly less important biological communities, such as those incorporating aquatic invertebrates, must be studied if a good understanding of the interrelationships amongst the physical, chemical, and biological environments is to be obtained. Continuous investigations of northern subarctic lakes and rivers would provide invaluable information on the effects that the northern climate might have on the productivity, species composition and diversity, life cycles, and energy flow in aquatic environments. Subsequent comparisons with terrestrial communities and similar aquatic communities of more southerly latitudes would greatly enhance our knowledge of the basic similarities and differences among all ecosystems.

Some information has begun to accumulate, thanks to the intensive efforts of such pioneers as the late D.S. Rawson of the University of Saskatchewan, who made several comprehensive limnological studies of northern lakes during the 1940's and 1950's (Frey, 1963). Ricker (1944,

1964) provides some distribution information on northern Plecoptera by combining collection records dating back to the turn of the century. Although there are a few studies pertaining to lotic and lentic environments in the north, life cycle data for aquatic invertebrates are especially lacking. The potential for life cycle studies, as suggested by my study, is substantial, given the abundance of aquatic insects and other invertebrates and the pristine conditions of virtually all the lakes and rivers. Major drawbacks to such studies involve the limited accessibility of most bodies of water during all seasons and the severity of the climate, with long periods of extremely low temperatures and thick ice cover in the winter and the frustrating ubiquity of biting insects in the short summer season.

My study represents an initial attempt at working out the life cycles of a few aquatic insects in a subarctic river; three basic questions can be asked. (1) What are some of the basic life cycle patterns of the insects studied in this area? (2) Which environmental factors affect these patterns, and how do they affect them? (3) How do the life cycle patterns observed in this region compare with those in other areas? These questions will be addressed by focusing first upon some physical and chemical factors and then looking at these in conjunction with the life cycle of each species studied.

Hynes (1970) has provided a good summary of factors known to control benthic invertebrates, and he included dissolved substances in his discussion. It would appear that none of the dissolved substances monitored in the Kakisa River seriously limits the benthic insect fauna. The Kakisa River is a small river with a slow to moderate current and hard waters. Although the current and other related conditions vary considerably during any year, these discharge-related phenomena do not appear to alter significantly the dissolved inorganic or organic constituents. The quantities of these substances, e.g. high oxygen levels, stable pH, low salinity, and high hardness, are not likely to be limiting in this type of river. Of all the dissolved substances studied, oxygen could have either the most significant influence on benthic insects or no influence at all. When present at very low levels (e.g. below 50% saturation), the effects can be limiting at best and devastating at worst (Britt, 1955; Lyman, 1956; Nebeker, 1972). When present at or near saturation, such as in the Kakisa River, oxygen apparently is insignificant in controlling the distribution of benthic insects (Hynes, 1970; Ulfstrand, 1967).

Life Cycles and Distribution

Pteronarcys dorsata

Life cycle. The life cycle of *Pteronarcys dorsata* in the Kakisa River can be summarized as follows: the eggs hatch in June; the nymphs grow over a 2-year period; there is a relatively short emergence period at the end of May and June; and the adults live for about 4 to 6 weeks after emergence. Data on egg deposition, possible egg or nymphal diapause, and growth rates are lacking. If *P. dorsata* has an extended egg diapause of up to 1 year, as shown for *P. proteus* by Dr. A. Miller in 1939 (Holdsworth, 1941), then *P. dorsata*'s life cycle could extend over at least 3 years. In fact, Holdsworth (1941) suggested that *P. proteus* may take up to 4 years to complete its life cycle, at least in

Massachusetts and under laboratory conditions. And Nebeker (1972) inferred at least a 3-year cycle for *P. dorsata* in his laboratory study of the effects of low oxygen concentrations on 2 and 3 year old nymphs. Similarly, Elder and Gaufin (1973) indicated a 3-year cycle for *P. californica* in the lower Provo River, Utah. Elder and Gaufin also suggested that if egg diapause was not obligatory, then oviposition by *P. dorsata*, which began at the end of May and lasted 3 weeks in Utah, could have accounted for a new generation by the end of June. The same may hold for *P. dorsata* in the Kakisa River, as indicated by the presence of newly hatched nymphs in June, coinciding with or shortly following emergence. This scenario would leave little time for an egg incubation period, suggesting instead rapid embryonic development.

Nebeker's (1971a, 1971b, 1972) data coincide with other aspects of *P. dorsata*'s life cycle in the Kakisa River. Nebeker's work on the effects of water temperature on feeding, emergence, and longevity can be summed up in the following quotation (Nebeker, 1971a, p. 25): "It can be concluded from this study that 15°C is optimum for feeding and emergence of this species. The temperature must be above 10°C and below 20°C for good adult emergence and egg production to occur." Nebeker (1971a) found that adult longevity was affected by the temperature at which nymphs developed, with nymphs kept at 10°C, 15°C, and 20°C developing into adults that lived an average of 36, 31, and 17 days, respectively. Nymphs kept at 5°C, 25°C, and 30°C did not transform into adults. Nymphs kept at 25°C and 30°C used most of the food consumed for maintenance rather than storing food for use in egg production or to maintain the adult stage for longer periods. Nymphs kept at 5°C showed no appreciable activity after 9 months at that temperature although they appeared healthy. Information obtained on *P. dorsata* in the Kakisa River agrees with Nebeker's data, Kakisa River nymphs apparently growing in 10° - 20°C water immediately prior to emergence and emerging in 1972 when the water temperatures were between 15° and 20°C; in 1973, emergence took place when the average water temperature was 15°C. Kakisa nymphs are seldom subjected to temperatures greater than 20°C (a few days at a time in July and August) and must certainly become quiescent over the 6 months when river temperatures are near 0°C.

Other studies have emphasized the influence of temperature on survival and emergence and sought to determine the effects of varying photoperiod and oxygen conditions. Nebeker (1971b, p. 779) showed that "the emergence of the large stonefly *P. dorsata* under constant light and constant temperature conditions indicates that normally increasing photoperiod and rising temperatures are not required." The importance of seasonally changing photoperiod in exerting some influence over emergence time was shown to be minimal under the laboratory conditions used. These conditions, albeit artificial, nevertheless took several factors into consideration in order to reproduce the natural conditions as best as possible. These studies therefore indicate that a combination of many factors regulate nymphal development and synchronize or otherwise influence emergence times. Branham, Gaufin, and Traver (1975) shed additional light on this subject by demonstrating that factors other than temperature and photoperiod had effects on survival, growth rate, and emergence for six stonefly species, including *P. californica*. Of the several variables listed, food was cited as quite important. Finally, oxygen was again shown to be of limited significance, as when Nebeker (1972) ascertained 30-day LC50's (median lethal concentration, for oxygen in this case) for 2 and 3 year old *P. dorsata* nymphs. The maximum 30-day LC50 obtained was 4.8 mg/1, well below the lowest concentration measured (8.2 mg/1) in the Kakisa River.

Distribution. *Pteronarcys dorsata* was found most often at station 5, indicating a habitat preference for rapid currents, considerable turbulence and very rocky substrata. Nymphs were often found in clumps under moderately large slabs of fractured bedrock, slabs anywhere from 25 cm to 80 cm in diameter. Larger rocks could not be lifted to determine if they served as substrate for the nymphs. Elder and Gaufin (1973) indicate that *P. californica* in the Provo River, Utah, inhabits similar areas, occurring commonly in dense aggregations in the larger streams. They found nymphs in swift water, but not "white" water, at water depths of 15 cm to 1 m. Nymphs found there seemed to prefer loose, unconsolidated bottoms with a minimum stone size of 15 cm. Given the largely herbivorous habits of these stoneflies, it was not surprising that they seemed to prefer loose rocks where allochthonous detritus collected. Elder and Gaufin found that *P. californica* nymphs also seemed to segregate by size (which I did not observe for *P. dorsata*) and migrated to shallower water just before emerging, a phenomenon observed for *P. dorsata* and especially *I. transmarina* in the Kakisa River. Richardson and Gaufin (1971) found that *P. californica* nymphs were found in medium-sized rivers in Utah and Colorado, mainly in trash piles and leaf packs lodged against rocks in midstream or under larger rocks near the shore.

Kamler (1967) found that the largest number of species of

Ephemeroptera and Plecoptera were found in slow and moderate currents (20 - 50 cm/s), while none were reported to inhabit exclusively torrential regions. Density of some species, however, was found to be lower in moderate current areas than in either slower or faster current areas. Current could be important in the Kakisa River especially if *P. dorsata* exhibits behavioral drift. Where suitable protection is not afforded nymphs, current and turbulence would tend to prevent their presence there; and in this respect, perhaps the plethora of rock slabs at station 5 makes this area the most suitable habitat with respect to both current and substrate.

Availability of suitable food sources is certainly an important factor with respect to the distribution of *P. dorsata* nymphs, and it is related to current and turbulence and the ability of substrate to support the appropriate flora or collect the appropriate detritus. As is true of *P. californica*, *P. dorsata* is herbivorous or, more probably, polyphagous. Hitchcock (1974), in the introduction to his monograph on the stoneflies of Connecticut, mentions a study by Harden and Mickel (1952) where *P. dorsata* nymphs were reared on dead elm leaves, which they reduced to skeletons. Perhaps this indicates the facultative nature of feeding habits of some stoneflies suggested by Richardson and Gaufin (1971). In their study about 80% of *P. californica*'s diet was detritus. Filamentous green algae, diatoms and animal matter were ingested as well. In fact, of the 275 specimens collected, 149 contained traces of animal matter. They suggested that the nymphs' diet might change with seasonal changes in abundance of food. If *P. dorsata* in the Kakisa River is a facultative polyphagous feeder, then food supply may not be a limiting factor with respect to microdistribution in the Kakisa River. Much of the lithophilic algae and accumulated detritus in the Kakisa River was found in the places where *P. dorsata* was also often found. But much algae and detritus were also found behind boulders, in deep holes, and regions of rooted aquatic plants; and these are areas in which *P. dorsata* was usually not found. Therefore it seems that a combination of habitat types, current conditions, and food availability are the most significant factors with respect to the microdistribution of *P. dorsata* nymphs in the Kakisa River.

Isoperla transmarina

Life cycle. In the Kakisa River, *Isoperla transmarina* has a univoltine life cycle, with either delayed hatching of summer-oviposited eggs or a nymphal quiescent period in winter, or both. Emergence takes place in late May and June. In addition to the work of Harper (1973) in southern Ontario, other studies on *I. transmarina* and related species give credibility to the patterns suggested for the Kakisa River populations.

Harper and Pilon (1970) worked with *I. transmarina* and *I. frisoni* in Quebec and found that "there might . . . exist a relation between the rate of increase of stream temperature and the synchrony of the emergence" (p. 689). As for the Kakisa population, emergence of *I. transmarina* in the Quebec stream took place during late May and early June, but the onset of emergence for *I. frisoni* in Quebec was retarded in colder years.

The effect of a stable and relatively constant environment was shown to be significant with respect to *I. petersoni* in Utah (Hales and Gaufin, 1971). The restricted habitat of moss in the cold spring-fed stream of Utah seemed to account for a short emergence period, although this association was not certain. It appeared that the constant, low water temperatures (5.5°C at source) had a different kind of influence on *I. petersoni*, a species with narrow tolerance limits, than on *Nemoura cinctipes*, a more broadly tolerant species in the same stream. *Nemoura cinctipes* uncharacteristically emerged throughout the year in the Utah stream. In contrast, the environment of Kakisa River is markedly variable, and the timing and success of all stages of *I. transmarina*'s life cycle would depend upon several factors and not just water temperature.

The life cycle of *Isoperla clio* in a small woodland stream in Kentucky (Minshall and Minshall, 1966) was found to be similar to that of *I. transmarina* in the Kakisa River. The major difference was in the time of onset of the various stages, especially the emergence period, with stages occurring a month earlier at the southern latitude. The Minshalls determined that the life cycle of *I. clio* was univoltine, with hatching taking place in late August and continuing into September. Nymphs grew slowly during autumn and early winter with the growth rate increasing at the end of February. Most nymphs were at least 10 mm in length by mid April and peak emergence occurred at that time. Egg deposition took place from April through June with the peak probably corresponding with emergence. This sequence of events would seem to parallel the suggested life cycle of *I. transmarina* in the Kakisa River, the life cycles of the two species being out of phase by about a month.

The life cycles of two *Isoperla* species in northern Sweden further demonstrate the effects of climate on aquatic insects (Svensson, 1966). *Isoperla difformis* exhibited considerable growth in late summer and autumn with no growth during the coldest months. Active development continued in March and April with emergence in May (flight period May 20 - June 20). *I. grammatica* grew fairly rapidly from August to October and slowly from November to April; the nymphs then increased in length rapidly and emerged in late June (flight period June 20 - August 7). Complete cessation of growth during the winter could not be demonstrated for this species, since no samples were taken during the coldest months. Ulfstrand (1968) found a different situation for *I. grammatica* in Swedish Lapland. Eggs hatched shortly after oviposition and nymphs started growing slowly, reaching a length of 2 - 3 mm in November. By May, the mean length had more than doubled with the remainder of growth taking place before the nymphs emerged, which took place in late July and August. The possibly more severe environmental conditions in Lapland, at 66° N, than in Svensson's study area, at 64° N, may delay various aspects of *Isoperla*'s life cycle there by a month or more. The general climatic factors affecting the life cycles of the Swedish species should correspond, within limits, to climatic factors affecting *I. transmarina*'s life cycle in the Kakisa River.

Distribution. The most suitable habitat for nymphs of this species appears to be the calmer and deeper water of station 2. The preferred habitat of *I. transmarina*, according to Harden (1942), is matted leaves and vegetation caught by submerged objects, a habitat type possibly provided best by the conditions found at station 2. This species was often found under relatively small stones (about 20 cm) in the Kakisa

River, especially during emergence when the nymphs migrated toward shallower water. Richardson and Gaufin (1971) found related species in similar habitats, with *I. fulva* living under stones, etc., in swift, well-aerated streams, and *I. elongatus* living under stones in riffle areas.

The same factors that regulate the microdistribution of *P. dorsata* nymphs probably also affect *I. transmarina*, the essential difference being the more carnivorous habits of *I. transmarina*. Nevertheless, food availability and its association with detritus would still be significant, since potential prey species probably prefer detrital matter as well. Egglishaw (1969) showed that the amount of plant detritus among stones was a significant factor in influencing the distribution of benthic organisms, especially stoneflies. *Isoperla fulva* and *I. elongatus* are primarily carnivorous, but ingest plant matter under certain conditions (Richardson and Gaufin, 1971). The gut contents of *I. fulva* contained about 69% animal matter and those of *I. elongatus*, about 65% animal matter. Probably *I. transmarina* has similar feeding habits.

Taeniopteryx nivalis

Life cycle. Eggs of *T. nivalis* are probably deposited in the early spring in the Kakisa River, with hatching taking place shortly thereafter, probably in late April and early May. Newly-hatched nymphs, or nymphs in early instars, would then go into a nymphal diapause until autumn when temperatures would be low enough to initiate a resumption of growth. Growth continues throughout the long winter, and emergence takes place shortly after breakup, in late April and early May. This would be the characteristic univoltine life cycle of a winter species, as demonstrated for *T. nebulosa* in northern Sweden (Svensson, 1966) and for *T. nivalis* in Canada (Robertson, 1967; Coleman and Hynes, 1970a; and Harper and Hynes, 1970). The reason why specimens of *T. nivalis* are very poorly represented in the Kakisa samples is probably due mainly to the inaccessibility of diapausing nymphs and lack of winter samples.

Harper and Hynes (1970) worked with several species of winter stoneflies, i.e. Capniidae and Taeniopterygidae including *T. nivalis*; they found that all winter stoneflies were univoltine; adult winter stoneflies, including *T. nivalis*, normally emerged in March and April when the ice began to break up. Harper and Hynes found that eggs were deposited in April and May and these hatched within a month. Some small nymphs could be found in May, but thereafter for most species, few if any nymphs were found until September. These September nymphs appeared to have grown very little in summer, most of the growth taking place subsequently in autumn and early winter. Summer diapause of these nymphs was considered to be an adaptation for survival at high summer water temperatures or for surviving the dry period in intermittent streams. Nymphal diapause was thought to have an advantage over egg-diapause, since nymphs could seek out suitable estivation sites, whereas eggs merely remained where they fell or were carried.

Coleman and Hynes (1970) showed that *T. nivalis* in a southern Ontario stream also had a simple univoltine life cycle. There was little growth during the warmer months, steady growth throughout winter, and emergence in March and April. This would correspond to *T. nivalis'* life cycle in Kakisa River, except emergence in southern Ontario is probably earlier, not surprising given the warmer climate there.

Ephemera simulans

Life cycle. Ulfstrand (1968, p. 177) states that "it is comparatively rare for Ephemeroptera to have life cycles covering more than one year." He stated that *Ephemera* spp. are often cited as having 2- or even 3-year cycles but he believed such evidence to be controversial. Hynes (1970) also reported conflicting evidence about 2-year cycles in a lake-dwelling species of *Hexagenia* and a river-dwelling species of *Ephemera*.

There are several studies pertaining to the life cycles of Ephemeridae. Three studies (Neave, 1933; Burks, 1953; and Lyman, 1955) indicate that *Hexagenia* takes 2 years to complete its life cycle. One study (Burks, 1953) implies that *Ephemera* takes 2 years as well, while two other reports (Speith, 1936; Lyman, 1955) conclude that *Ephemera*, in lakes, completes its life cycle in only 1 year.

I believe that *E. simulans* in the Kakisa River, and possibly *H. limbata* in Kakisa Lake as well (Lamoureux, 1973), has a life cycle of at least 2 years. The peak emergence of *Ephemera* adults occurs in mid to late June, with total emergence extending over May, June, and early July. Egg deposition and death of adults coincide with emergence, with newly-hatched nymphs appearing in late July and early August. Growth of nymphs is most rapid in spring and early summer with a general slowing or even cessation of growth during winter. Different environmental conditions from year to year, particularly changes in temperature regime, probably affect the phenology of certain life cycle events. Emergence, for example, appeared to take place somewhat earlier in 1973 than 1972 in Kakisa River, and this corresponded with an earlier onset of spring conditions (earlier snow melt, breakup) in 1973.

Many of the interpretations made about the life cycle of *Ephemera* were based on total body length being an indication of developmental stage. For *Leptophlebia cupida*, Clifford (1970a) found that an increase in nymphal size could not be strictly related to development, since larger nymphs are sometimes physiologically younger than smaller nymphs. Relative growth methods have shown how *Leptophlebia* nymphs develop with changes in size, particularly as related to changes in total length (Clifford, 1970b). These methods might be applied to *E. simulans* in the Kakisa River. For example, after nymphs reached a length of about 15 mm, no clear-cut relationship between wing pad coloration and total length could be made, thus confusing any attempts at predicting readiness to emerge or assessing overall growth and development. In any event, linear measurements of *E. simulans*, particularly total length, are probably as variable with absolute age as those of *L. cupida*, especially considering that sexes were not measured separately. Also, killing and preserving specimens can change their body length, especially if they have been damaged by sampling or sorting. Britt (1953) showed that killing specimens of *E. simulans* in KAAD, a mixture of one part kerosene, seven to ten parts 95% ethyl alcohol, two parts glacial acetic acid, and one part dioxane, and preserving them in 95% ethyl alcohol increased their total length considerably. Kakisa River specimens were killed in weak formalin, stored in that liquid for a short time, and ultimately preserved in 98% ethyl alcohol. Perhaps some change in length might have occurred in these specimens as well. But these changes were probably insignificant, occurring in all size classes and therefore not influencing appreciably the life cycle analysis.

All immature nymphs collected within the study area were *E. simulans*; but during emergence periods, which could have overlapped for both species, floating nymphs and subimagoes of emerging *H. limbata* and *E. simulans* could have occurred together. Subsequently, the swarms of adults seen flying above the river during summer evenings could have included both species.

For more temperate climates, life cycles and general ecology of both *E. simulans* and *H. limbata* have been thoroughly investigated. A comparative overview of some of these studies including the Kakisa study is presented in Table IX. There are major phenological differences between studies, especially in emergence. For example, there is a difference of about 2 months between the earliest and latest emergence periods, with no general north to south trend. Overall climatic differences probably exert some influence, but local factors appear to be important. Local variations in weather patterns, especially as they affect water temperature, and the combination of a variety of other factors must certainly alter life cycle patterns rather than any single factor or condition. Table IX shows that swarming begins later in the day the farther north the species are found, ranging between 2000 hours at Lake Erie to 2400 hours in the Northwest Territories.

Finally, mention should be made of the strong probability of variable growth rates of nymphs. One of the more obvious features of the Kakisa samples was the wide range of size classes of *E. simulans* nymphs in any sample. This can probably be accounted for by the variable growth rates

Table IX. Comparison of *Ephemera* (E) and *Hexagenia* (H) life history data from different regions.

TABLE IX: COMPARISON OF EPHEMERA (E) AND HEXAGENIA (H) LIFE HISTORY DATA FROM DIFFERENT REGIONS

AUTHORS & THEIR REGIONS		TIME OF EGG DEPOSITION	TIME OF HATCH	PERIOD(S) OF SLOW OR NO GROWTH	EMERGENCE PERIOD (TOTAL)	PEAK OF EMERGENCE	TIME OF SWARMING	LIFE SPAN OF ADULTS	LENGTH OF LIFE CYCLE
°BURKS, 1953 ILLINOIS	E		1-2 weeks after deposition		occasional specimens, April - October	early June		2 or 3 days	possibly 2 years
	H		1-2 weeks after deposition		occasional specimens April to October	late June or July		2 or 3 days	2 years
°FREMLING AND KLOEK, 1969 CENTRAL MINN. & N. WIS.	E				earliest: 5/22/62 latest: 7/22/63	last 3 weeks in June			
	H								
°FREMLING & KLOEK, 1969 N. MINNESOTA	E					last week of June - 1st wk. of July			
	H								
°LYMAN, 1944 W. end LAKE ERIE	E								
	H				end of June to September	during July	20:00 hrs. EST to after dark		
°LYMAN, 1955 DOUGLAS L. MICHIGAN	E		probably late July and early August	winter - November to Spring (probably)	June 10 - August 1	early to mid July			one year
	H	late June - early July	prob. last of July, early August	prob. slow or no growth in winter	June 15 - July 20	June 20 - July 5	21:00 - 22:00 hrs. EST		two years
°MUSBACH 1972-1973 KAKISA RIVER, N.W.T.	E	prob. late June - early to mid July	last of July - early August	over winter: October - April	probably May - July	mid - late June, perhaps into July	midnight (dusk)		two years
	H				probably May - July	mid - late June, perhaps into July	midnight (dusk)		
°NEAVE, 1933 L. WINNIPEG MANITOBA	E								
	H	July	August	little or no growth over winter	from June 20 to end of August	mid July	21:00 - 22:00 hrs. (CST?)		two years
°PETERS AND WARREN, 1966 NW. ARKANSAS	E				first of May - mid June	mid May			
	H				early May - end of August	late June			
°SPEITH, 1936 L. WAWASEE INDIANA	E	late May - early June	probably 20-30 days after deposition			last of May - 1st few days of June	(late May)		one year
	H								

of nymphs in any one generation, as well as by the presence of overlapping generations. Speith (1936) found that in samples which included at least 22 individuals, the smallest specimen of *E. simulans* was half the length of the longest, with the disparity often being greater. Neave (1933) found what was apparently an overlapping in size of the largest first-year nymphs and the smallest second-year nymphs of *H. limbata occulta* in his June samples. He attributed this to varying growth rates, which resulted from differences in bottom type, food availability, competition, and other localized conditions.

Distribution. Studies of Lyman (1956), Eriksen (1968) and Cummins and Lauff (1969) provide good information on substrate as a factor in the microdistribution of Ephemeridae nymphs. These studies establish that *Hexagenia* and *Ephemera* nymphs have different requirements. Cummins and Lauff (1969) indicate that *E. simulans* nymphs favor sand and gravel substrates and avoid finer sediments. Eriksen (1968) states that "it appears that *H. limbata* is not found in streams unless prevailing conditions include at least undisturbed, fine sediments, in which burrows can be maintained open to the substrate surface, for *Hexagenia* does not burrow into coarse substrates. To the contrary, *E. simulans* can thrive in gravel and pebble stream substrates . . ." Lyman showed that mud was preferred by *H. limbata* and that sand was avoided by *H. limbata* and probably *E. simulans*. Sand apparently offered too much resistance to these burrowers and the sand grains tended to fall back into the burrows. None of these studies conflicts with my findings that the largest proportion of *Ephemera* nymphs were found at station 2, which has a diverse substrate, probably allowing successful burrowing in several places.

The different preferences of *H. limbata* (mud) and *E. simulans* (gravel, coarse sediments) could possibly be a factor influencing their ecological segregation in the Kakisa area. *Hexagenia limbata* nymphs are found almost exclusively in the silt-bottomed sublittoral areas of Kakisa Lake (Lamoureux, 1973), while *E. simulans* is restricted to the more stony and riffle-like environs of the river. Where the two species occur in close proximity, such as the outlet area of Kakisa Lake, other factors must be important. Lyman (1956) discusses oxygen as a limiting factor for *H. limbata* in Douglas Lake, Michigan. But dissolved oxygen as a factor in distribution is probably not important for either *H. limbata* in Kakisa Lake or *E. simulans* in the river, since both environments appear to be well-oxygenated the year round. I believe that the microdistribution of *E. simulans* is most influenced by substrate.

Ophiogomphus colubrinus

Life cycle. It was only possible to determine certain features of *Ophiogomphus*' life cycle. The emergence period was obvious, even without an organized sampling effort, the adults emerging in large numbers during a very short time. Emergence is well-synchronized, taking place over 4 days during mid to late June. Adults live for several weeks, and females deposit eggs a few weeks after emergence. I saw one pair *in-copula* 3 weeks after emergence. Newly hatched nymphs appear in the latter part of July. Delayed hatching or retarded growth may also be indicated, since 3 and 4 mm nymphs were found in early May, 1973. As has been previously stated, the small sample size, considerable size range of nymphs present in any sample, and lack of rearing experiments render any determination of growth patterns and overall life cycle impossible. The life cycle probably takes at least 2, and possibly up to 4, years.

Considerable variation in habits and time of events is apparent for a few species of this genus. Kennedy (1916) found that emergence of *O. severus* Hagen began in the second week of June and continued until the first week of July in Satus Creek, Yakima Valley, Washington. Emergence took place during the day, the nymphs, unlike Kakisa specimens, seldom crawling more than 15 cm from the water to emerge. Oviposition for *O. severus* took place in August.

Ophiogomphus probably has a long adult life span, given anonymous records cited by Whitehouse (1948) of the length of the periods that adults were seen in flight in various regions of Canada: *O. rupinsulensis* (New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan), fourth week of May - fourth week of September; *O. severus severus* (Saskatchewan, Alberta), fourth week of June - second week of September; *O. severus montanus* (British Columbia mainland), second week of June - first week of September; and *O. colubrinus* (Newfoundland, Quebec, Ontario, Alberta, Saskatchewan, Manitoba, British Columbia mainland, and the Northwest Territories), third week of June - first week of September.

Factors Affecting Distribution

This section is concerned primarily with the microdistribution of nymphs within streams. Although a separation of endogenous and exogenous factors is difficult, the discussion will briefly outline the important physical aspects of the environment that influence microdistribution. Not only such factors as discharge, current, temperature, food availability, and substrate will be discussed but also habitat and food preferences, morphological adaptations, temporal separation (seasonal succession), competition, predation, species composition and diversity, and adult behavior. These factors may have caused the consistent disparities in numbers between stations (Table IV) and may be significant.

Sampling Technique

A kicking technique similar to that described by Frost, Huni, and Kershaw (1971) was employed in the Kakisa River. They stated that inadequacies of such a technique are related to a variety of factors, including number of times applied at any site, current, size of substrate material, and nature of the fauna. Any sample will often poorly represent the benthic fauna, both in terms of species composition (relative diversity) and numbers, because of these and other factors. In fact, it was shown that "small samples have consistent percentage population components differing significantly from large ones" (Frost, Huni, and Kershaw, 1971, p. 171). The small Kakisa samples might therefore be poor representations of reality, and inconsistencies between samples could have occurred, with "good" and "bad" days resulting from different weather conditions, discharge volumes, and turbidity. Furthermore, Coleman and Hynes (1970b, abstract and p. 37) showed that "significant numbers of animals occur deep within the substrate of stony streams, and that even samples collected down to 30 cm do not adequately represent the fauna." Such organisms are apparently capable of considerable lateral movement as well. Most significantly, when a comparison of sampling techniques was made, it was found that kick samples, which cannot sample the hyporheal zone, contained proportionately fewer of the very small animals. Such under-representation could have occurred in the Kakisa River, although bedrock lies close to the surface of the river bottom in many places and constitutes the entire substrate in a somewhat fractured form in a few locations.

Drift

The effects of nymphs drifting downstream could have had both short- and long-term implications. I assume that drift does not have a devastating effect on the population as a whole and that the disparities in numbers between stations were not caused by drift of any type, or at least not by drift alone. Constant drift certainly cannot be of major significance, since the fauna existing in the river is obviously adapted to it and disparities in numbers and other fluctuations would not be accounted for by it. Behavioral and catastrophic drift probably are significant, however, given the dramatic fluctuations of shallow Kakisa Lake. Ephemeroptera and Plecoptera are known to exhibit behavioral drift and it has been shown that the night:day drift rate ratio was greater during periods of higher discharge (freshets) than during periods of normal or lower water flow (Anderson and Lehmkuhl, 1968). If the benthic fauna of Kakisa River exhibit a similar type of behavioral drift periodicity, then the often rapid fluctuations in discharge would certainly bring about a loss of nymphs from the local population at those points in the fluctuations where current or volume of discharge is greatest. Behavioral drift by itself, in Kakisa River (i.e. over periods of stable flow), may not be very significant to the population structure of the benthic fauna and may resemble constant drift in general effect over extended periods. This would hold true unless certain nymphs are more susceptible to drift than others. Anderson and Lehmkuhl (1968, p. 205) indeed found this to be the case where, in a small stream in Oregon, "larger individuals of Ephemeroptera, Plecoptera, and Diptera occur in night drift as compared with the day and also under high water conditions as compared with low water." They also found that mean weights of nymphs in drift samples were consistently greater than in benthos samples, and particularly greater at night than during the day and in freshet as compared to non-freshet periods.

Catastrophic drift has been shown to be significant in terms of changes in drift rate rather than drift density (Anderson and Lehmkuhl, 1968). Drift rates were shown to increase during freshets but the density of animals in the drift was not significantly greater during freshets than during non-freshet periods. The drift rate was also shown to drop rapidly after the water levels subsided, with normal drift rates resuming within 24 hours after the rains stopped. If this situation applies to nymphs in the Kakisa River, then few samples would show the effects of short-term changes in discharge, most sampling having been done under conditions of easy and comfortable access to the river, when currents and water levels were stable. The effects of longer term changes in water level than those caused by rain and wind, and the effects of fluctuating turbidity (turbid conditions perhaps equalling night to nymphs), will not be discussed here.

Aquatic insects must be morphologically and physiologically adapted to the environmental anomalies of Kakisa River and well-equipped to survive the rigors of all discharge-related factors. Hynes (1970), in his comprehensive work on lotic environments, discusses a variety of adaptations. Certainly the burrowing capabilities of *Ephemera*, with its mandibular tusks and moveable gills for use in burrows, and the well-sclerotized and flattened condition of the Plecoptera and gomphid nymphs enable them to avoid the detrimental effects of current, especially living as they do under well-settled rubble.

Substrate and Food

Substrate type and stability and food availability are two very important factors influencing the microdistribution of benthic nymphs and ultimately the life cycles of the species. Ulfstrand (1967) emphasized the importance of these two factors while also stating that a combination of factors, rather than any one factor acting alone, is most important to nymphal distribution. His study is particularly relevant here, given the similarities between his Lapland research areas and the Kakisa environment. The close association of factors was also made obvious by Egglishaw (1969) who showed that one of the chief sources of available plant food for Plecoptera in fast-flowing British streams was plant detritus among stones. For this reason the amount of plant detritus was the factor with which most of these invertebrates were associated. Similarly, Cummins and Lauff (1969, p. 170) indicated that while *E. simulans* nymphs apparently favor sand and gravel substrates and can be described generally as gravel insects of intermediate stream habitats, it was also apparent that the exact limits of microdistribution were set by other parameters. They stated that the nature and abundance of detrital food substances were important.

Predation

Predation is probably a controlling factor for most of the species studied and may limit their distribution within certain areas of the

Kakisa River where protection is scarce and predators abound. Above the waterfall in the deeper and less turbulent sections of the river, fish species from Kakisa Lake are found, particularly lake whitefish (*Coregonus clupeaformis*). This species ate a large proportion of mayfly nymphs in the lake (Lamoureux, 1973), particularly *Hexagenia*, and must certainly have consumed ephemerids in the area of the river below the lake outlet and well above the falls. Mayflies would have been especially vulnerable during the emergence period when large numbers of subimagoes were floating down the river. Arctic grayling (*Thymallus arcticus*) and long-nosed suckers (*Catostomus catostomus*) spawn below the waterfall in mid spring and their presence in this stretch must account for some invertebrate predation. The relative paucity of stonefly nymphs in particular at station 4 (upper limit of spawning run) may have been the result of predation in part, although human disturbances at this tourist site could also have been significant. Other fish species such as the slimy sculpin (*Cottus cognatus*), walleye (*Stizostedion vitreum vitreum*), and northern pike (*Esox lucius*) may also prey upon benthic invertebrates, invertebrates in the drift, and emerging adults. Finally, other aquatic insects, such as predatory dytiscids and the gomphids, may prey upon the smaller nymphs of all species studied. The exact nature of predator-prey relationships in the Kakisa River is virtually unknown except for some tentative information obtained on fish during a limited creel census undertaken by Fisheries Service personnel (1972).

Other Factors

Other factors affecting the distribution of nymphs and even adults within the study area relate directly to resource exploitation.

Population size, species composition, and species diversity are limited by the carrying capacity of the environment, by several ecological factors among which are food availability and type and suitability of the habitat. Generally, if cohabitant species are not closely related (i.e. have dissimilar sustenance and spatial needs), their survival will depend upon the richness or complexity of the environment; if such species are closely related (i.e. with similar sustenance needs), ecological segregation by temporal means is probably necessary. Grant and Mackay (1969, p. 693) have suggested that ecological separation of closely related species by habitat is relatively weak; systematized patterns of resource exploitation have evolved, where "natural selection has favored a difference in the time at which the maximum impact upon the resources is made by each species, i.e. the maximum energy flow through them is temporally staggered." If temporal segregation is not possible, then other patterns of exploitation would have to be used in the avoidance of interspecific competition. With the exception of the winter species *Taeniopteryx nivalis*, there appears to be little or no seasonal succession of the species studied and there is a lack of congeneric species as well. The short summer season that most species must utilize for growth and emergence would therefore suggest patterns of resource utilization other than temporal separation. Such patterns may incorporate different habitat preferences, general habitat selectivity, possibly significant associations of species (Knight and Gaufin, 1967), longitudinal succession (Kerst and Anderson, 1975), and the ability of the environment to sustain in relatively large numbers a few key species of invertebrates that may have similar requirements.

The Boreal Environment

In this final section some tentative conclusions about the life cycles of subarctic aquatic insects will be made. I will discuss (1) the important features of northern subarctic environments as they affect a river and its fauna and (2) the general life cycle patterns of this environment.

Important Factors

Temperature, alone or in concert with photoperiod, would seem to be one of the most, if not *the* most, important factor affecting life cycles of northern aquatic insects. The overall temperature regime of a region appears to have a marked influence on nymphal growth (Brinck, 1949; Svensson, 1966), time and synchronization of emergence (Harper and Pilon, 1970; Nebeker, 1971c; and Kerst and Anderson, 1974), and the life cycle patterns as a whole (Brinck, 1949; Hartland-Rowe, 1964; and Clifford *et al.*, 1971). Nevertheless, while temperature may be of utmost importance, it would never be the sole operant in any environment. Ulfstrand (1968) acknowledged the importance of temperature (particularly local temperature differences) but indicated that a variety of factors influence life cycle patterns. One of these factors, photoperiod, may have as significant an influence on the life cycle as temperature.

The relative importance of both temperature and photoperiod can be demonstrated by discussing one stage of an aquatic insect's life cycle, the emergence period. Nebeker (1971c) showed that temperature and photoperiod varied in importance in the regulation of emergence patterns of certain stoneflies in a canyon stream in Utah. In some areas of the stream, temperature was the major influence on emergence patterns (with emergence delayed by several months in the colder waters at higher elevations), even though photoperiod may have been the initial stimulus. In other reaches (presumably springs), photoperiod was the main regulator of emergence time. In addition to their role in the regulation of time of emergence, both temperature and photoperiod probably are responsible, at least in part, for the synchronization of emergence observed in many stoneflies and mayflies (Kerst and Anderson, 1974). Temperature would set the general seasonal time of emergence (by regulating nymphal development), and then photoperiod would account for the specific synchronization within that period.

Harper and Pilon (1970) list five factors that are probably the determinants of emergence: (1) temperature, (2) internal regulating mechanisms that synchronize the population at the onset, during the course of, or at the end of larval growth, (3) embryonic and larval diapauses, (4) photoperiod, and (5) resynchronization at the end of larval growth. Possibly all of these factors are necessary in the regulation of emergence for any given species. For example, temperature and photoperiod may act in unison, at least just prior to emergence, and even control the other factors. Regardless, temperature and photoperiod are certainly the most rhythmically (seasonally) changing in the north.

Finally, there is the possible significance of biological factors within a population itself in the determination of readiness to emerge and time of emergence. Endogenous factors, while under the influence of the external environment, may nevertheless operate more or less independently to ensure the synchronization of emergence of a generation. Clifford (1970b) suggests that *Leptophlebia cupida* nymphs for which simple size allometry holds are generally "immature" and that deviation represents a transition into a "mature" state. Consequently, nymphs are accumulated in the "mature" stage in spite of variations in size, thus promoting a synchronized emergence. Even though information is lacking, the possibility of such a synchronizing mechanism seems strong at least for *E. simulans* in the Kakisa River and perhaps also for some of the other insects of the river.

I conclude that the factors influencing both microdistribution and life cycle patterns in this northern river are difficult to separate, even though a variety of factors have been identified and considered significant for both aspects of the ecology of aquatic insects. Specific factors regulating microdistribution, whatever they are, most certainly account for where a species will occur within a river, in what numbers, and even how long it will exist there. And specific factors determining life cycle patterns most certainly have the general effect of determining when specific stages of the species will occur. In the Kakisa River, temperature and photoperiod are probably the most important factors with respect to the determination of life cycle patterns for the aquatic insects.

Life Cycle Patterns

To characterize the life cycles of the Kakisa River species, it is useful first to summarize the phenological categories or types that have been established by other workers. According to Ulfstrand (1968), such categories have been developed as a way of classifying benthic insects for ecological analysis. They have been particularly useful in the analysis of the life cycle patterns from various climatic regions. Some of these phenological classifications are given below.

1. Macan (1965) and Hartland-Rowe's (1964) classification:
    - A. development of one generation taking longer than one year
    - B. more than one generation in one year (multivoltine)
    - C. one generation in one year (univoltine)
        - 1. summer species — eggs hatch and development completed in summer; species overwinters as adults or eggs
        - 2. winter species — overwinter as larvae; disappear or become scarce at some time in summer
            - a. hatching in late summer and some growth in autumn; no growth in winter; growth resuming in spring with development completed in summer
            - b. egg laying and hatching in spring; growth through summer, autumn, and more slowly in winter; more rapid growth and emergence in spring
2. Landa's (1968) classification:
    - A. one generation in a year
        - 1. winter species — nymphs hatch in summer and autumn, continue to grow throughout the winter and emerge the following spring or summer
        - 2. summer species — nymphs hatch, grow and emerge during a short period of summer, the eggs being in a supposedly diapause state for most of the year
        - 3. winter species — nymphs hatch and grow in summer and autumn, but not in winter, growth resuming in the following spring
    - B. two or more generations in a year
    - C. one generation in two or more years
    - D. others
3. Ulfstrand's (1968) classification (Swedith Lapland):
    - A. one-year cycles
        - 1. considerable growth commencing shortly after oviposition leading to the presence of more or less large-sized nymphs during a long period
        - 2. intense growth concentrated to a period preceding emergence
        - 3. egg and larval stages short, pupal stage long (species other than plecopterans and ephemeropterans)

B. two-year cycles
    1. considerable growth before and during (part of) first winter
    2. first winter spent as egg or as more or less quiescent early nymph

C. three- and four-year cycles

4. Brinck's (1949) classification (specific for Plecoptera):

A. hiemal — species growing during autumn, winter, and spring (2 types)
    1. growth in autumn and winter; emerging late winter or early spring (e.g. winter stoneflies)
    2. growth begins in autumn, usually slightly retarded in winter, and continues in spring

B. estival — species growing during late spring and summer.

In addition to these phenological outlines, some further characterizations and distinctions have been made. Ulfstrand (1968) distinguishes between diapause and quiescence and defines dormancy. Diapause is defined as an endogenous arrestment of growth, whereas quiescence is defined as an exogenous arrestment. Dormancy is referred to as an egg state where no development seems to take place for some time after deposition. Also, Hartland-Rowe (1964) and Radford and Hartland-Rowe (1971) describe seasonal life cycles in terms of slow-seasonal and fast-seasonal cycles. A slow-seasonal cycle is when the eggs hatch soon after deposition and larval growth is slow and steady over a long period. In the fast-seasonal cycle there is rapid growth after a long egg-diapause or during the second generation of a bivoltine species.

Certain life cycle stages can also be described as types of patterns. Harper and Pilon (1970), in their work with some Quebec stoneflies, described two types of emergence patterns: (1) a short synchronous emergence typically concentrated at the beginning of the period with 90%

of the population often emerging within the first few days; and (2) an extended (asynchronous) emergence where the rate of maturation is more gradual and emergence proceeds slowly, e.g. about 50% of emergence is reached midway through the period. In both types, intensity of emergence is the key factor and not the total length of the period.

Using any of the above phenological schemes, the Kakisa species can be readily categorized. *Pteronarcys*, *Ophiogomphus*, and *Ephemera* (and probably *Hexagenia*) all appear to have life cycles that take more than 1 year to complete. *Pteronarcys dorsata* probably takes at least 2 years, but maybe 3 years if there is a year-long egg-diapause. *Ephemera simulans* probably takes 2 years, and *Ophiogomphus colubrinus* takes at least 2 years to complete the life cycle. *Taeniopteryx nivalis* and *Isoperla transmarina* are univoltine species in the Kakisa River, and both would seem to be winter (or hiemal) species. *Taeniopteryx* is certainly a winter species, growth occurring in the winter and emergence taking place in early spring when the ice breaks up. *Isoperla* is probably also a winter species, but with most of its growth taking place outside of the coldest months. *Isoperla* obviously must restrict much of its growth and development to the short summer period, but this does not necessarily infer an estival (or summer) pattern. If an estival pattern did exist, then *Isoperla* would likely be in an egg-diapause state much of the year (at least October through early April), but this has not been demonstrated. In fact, nymphs do appear to grow over the winter months — some have been found in February -- although, again, extensive quiescent periods are probable. *Isoperla* would then seem to be just one of many winter species that have little or no growth in winter, a situation demonstrated for many of the mayflies studied by Clifford *et al.* (1971) in Alberta.

To characterize any of the Kakisa species as either fast- or slow-seasonal would be difficult, at least for those species with one generation extending over at least 2 years. There is no evidence for diapause, although it could exist in some species, and overlapping generations and a wide range of size classes being present at any given time confuse things further. Perhaps the two categories are insufficient to describe the growth patterns of species having life cycles that take more than one year to complete. Perhaps a combination of both types of seasonal patterns is possible for these long-lived species.

The univoltine species, however, give some indication of having more definite seasonal cycles of growth according to Hartland-Rowe's (1964) categories. *Isoperla transmarina* is of the slow-seasonal type, even though it may have at least a month-long egg dormancy after deposition. In contrast, *Taeniopteryx nivalis* has a fast-seasonal cycle. These categories may be somewhat arbitrary and at best only partially accurate, but such characterizations are useful in comparing growth rates and general life cycle patterns.

The type of emergence pattern observed for all the Kakisa species is synchronous. Data for *Pteronarcys*, *Isoperla*, and especially *Ophiogomphus* nicely show this. *Ephemera* may have a more extended emergence pattern, but until quantitative collection of emerging adults is undertaken no firm conclusions can be made. The mechanisms involved in synchronization are not known. And in this regard, water temperature and photoperiod should also be investigated thoroughly in the boreal region, where daily river temperature fluctuations can be considerable and the light regime differs dramatically from that of more southerly latitudes. There is some evidence that emergence periods for most species occurred about 1 or 2 weeks earlier in 1973 than 1972, and ~~this~~ may have been related to water temperature, the river warming up sooner in 1973 than 1972.

Final Remarks

Inevitably, an ecological understanding of any environment, of any community or ecosystem so designated, is inadequate or incomplete if it does not take into account the presence of man. The direct and indirect effects of man on the environment are everywhere and to assume some kind of ecological "purity" or community isolation from them is at best unrealistic.

The possibility of hydroelectric development on the Kakisa River weighed heavily on my empirical perspective. The proposed impoundment was to have been constructed, and still might be, in the middle of the study area and would have affected as much as half the Kakisa drainage basin. This development would dramatically affect the biota of the watershed, aesthetics of the region, and the life style of the native population. In this era of the omnipresence of man, particularly Western industrial man, such development of a relatively pristine environment must be given serious forethought. Certainly no study, or group of studies, has to date provided a completely holistic view of the Kakisa environment, with projections of long-term goals, trends and possibilities; and none seems to have dealt satisfactorily with the question of why the dam must be built in the first place. Aside from the energy-source needs of Pine Point Mines, which is over 150 km away, and the establishment of a link between Pine Point and Yellowknife in an electrical power system, this remains an open question. It is to this question and the implicit alternatives that we must address ourselves before a substantial portion of an important drainage system is drastically changed.

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APPENDIX I

Mysis relicta

Mysis relicta (Crustacea: Peracarida), more typically known from deep oligotrophic lakes, has been found in small numbers in Kakisa Lake (Lamoureux, 1973, p. 25). *Mysis* was also found in the stomach contents of some fish (Christiansen, pers. comm.) and I found it in drift samples of May 8 - 9, 1972, and May 15 - 16, 1972, at the lake outlet and at station 2. Drift samples contained only a few specimens, and this, along with Lamoureux's (1973) data, suggests that *Mysis* is probably rare in the lake. Larkin (1948) found *Mysis* in Athabasca, Great Bear and Great Slave Lakes; he studied it extensively in Great Slave Lake, where it occurred in large numbers. This would be expected, given the great depth, low water temperatures and generally oligotrophic nature of these lakes. As far as is known, *Mysis* has not yet been found in the Northwest Territories in shallow, isothermal and near-eutrophic lakes other than in Kakisa Lake.

APPENDIX II

Plecoptera of Kakisa River

Alloperla - identification uncertain

Claassenia sabulosa (Banks)

Frisonia parallela Ricker

Hastaperla - identification uncertain

Isogenoides colubrinus (Hagen)

Isoperla transmarina (Newman)

Pteronarcys dorsata (Say)

Taeniopteryx nivalis (Fitch)

All species were identified from nymphal and adult specimens.